

KIRTLANDIA[®]

THE CLEVELAND MUSEUM OF NATURAL HISTORY

CLEVELAND, OHIO

NUMBER 29

PLIOCENE-PLEISTOCENE SUIDAE FROM HADAR, ETHIOPIA

H. B. S. COOKE

Dalhousie University
Halifax, Nova Scotia, Canada

ABSTRACT

Three different suids occur in the Hadar Formation. *Nyanzachoerus pattersoni* is plentiful in the Sidi Hakoma member, especially in the lower part, and morphologically matches the type material from Kanapoi very closely. *Notochoerus euilus* ranges throughout, making up 61% of the total sample. The skull architecture is described for the first time. A small suid occurring throughout is regarded as a new species of *Kolpochoerus*, *K. afarensis*, distinguished from *K. limnetes* by its smaller size, simpler molars and more *Sus*-like features of the premolars. It is, in all probability, ancestral to *K. limnetes*. Comparison of the *Notochoerus euilus* material with that from the Usno Formation and the lower part of the Shungura Formation suggest that the lower Sidi Hakoma member may be in the range of 3.0 to 3.5 million years old.

INTRODUCTION

Addis Ababa, the capital of Ethiopia, lies in the center of the country at an elevation of 2,355 metres above sea level, not far from the source of the Awash river. This river drains northeastward into the Afar province, but derives much of its water from the highlands near the source area and from seasonal streams that flow into it from the western flanks of the Afar triangle. One of these streams, Kada Hadar, meets the Awash in an area that has yielded substantial amounts of fossil material, including important hominid remains (Taieb et al., 1972; Taieb, Johanson and Coppens, 1975). The broad framework of the geology has been considered by Taieb (1974) and the particular succession

exposed in the Hadar area has been described recently (Taieb et al., 1976), together with a preliminary account of the fossil remains and hominid discoveries (Johanson and Taieb, 1976). The Awash at Hadar is close to 500 m above sea level, with local relief of some 100 m and badland type dissection.

The Hadar Formation has a thickness of about 180-200 m, although the base of the lowest unit is not yet firmly established. The sediments are largely arenaceous and argillaceous and represent various phases in a fluctuating complex of lacustrine, lake margin and fluvial deposits, apparently related to a Pliocene-Pleistocene lake that occupied much of the Afar basin. Several minor erosional unconformities can be seen, but they do not appear to represent major breaks. A few steep normal faults, with displacements of 5 to 40 m occur. The Hadar Formation is capped unconformably by an unnamed unit of Pleistocene gravels and sands that contain hand axes.

The Hadar Formation has been divided into four members, conveniently separated by volcanic tuff horizons that are laterally extensive and usually altered to a chalky white material, forming useful "markers." The lowest tuff complex (SHT) divides the Basal Member (BM) from the Sidi Hakoma Member (SH) and in places it has been preserved in channels, where the material is not altered and consists largely of fresh glass shards. The Sidi Hakoma Member has been subdivided into four submembers (SH-1, SH-2, SH-3, SH-4) and within the upper submember there is at the eastern end of the Hadar area a magnetically reversed basalt flow, 1 to 4 m thick, that dies out towards the northwest. Its resistance to erosion resulted in the development of a minor plateau in this area, capped directly by the Pleistocene gravels. Preliminary K/Ar determinations on the basalt give ages of 2.9 ± 0.2 m.y. and 3.0 ± 0.2 m.y. (Aronson et al., 1977). The TT marker lies 20 m above the basalt level and is a very persistent zone of thin tuffs defining the base of the Denen Dora Member (DD); within this member, three submembers are recognised (DD-1, DD-2, DD-3). The KHT tuff is a single deposit that is laterally less extensive than the older tuffs but serves to define the base of the fourth member, the Kada Hadar Member (KH). Like the SHT tuff, it occurs also in channels where glass shards are well preserved. Four submembers have been recognized within the Kada Hadar Member (KH-1, KH-2, KH-3, KH-upper), although the validity of these divisions has more recently been questioned (Johanson, et al., 1978). About 9 m above the KHT tuff is another distinctive marker, CC, consisting of a green argillite that produces small flakes as a characteristic alteration product of weathering.

The occurrence of complete and partial skeletons suggests rapid deposition, in a relatively low energy environment. The preservation is usually excellent, with some specimens looking almost like fresh bone, but many are

encased in a thin layer of hard calcified mud that may make cleaning and preparation difficult. Nearly all the specimens are surface finds, but their condition makes it clear that they have not been transported for any significant distance and the range of uncertainty regarding the horizons of derivation is usually small. However, it is not always possible to place material within one of the submembers, so localities which lie close to a boundary are designated by recording the two possible units (eg. DD2/3). The fossil localities are assigned numbers, prefixed by "AL" and each specimen from that locality is given an individual number (for example, the hominid skeleton "Lucy" is AL 288-1). The stratigraphic positions at present assigned to those localities that have furnished suid remains are indicated below. As will be seen, there are many localities in SH-1 to SH-3 and again in DD-1 to DD-3, but relatively few in SH-4 and in KH-1 to KH-3. It is convenient to group the suids stratigraphically into four divisions as follows:

- D. Lower Kada Hadar Member, together with two localities which span DD-3 and KH-1; includes localities: 120, 157, 164, 186, 310, 359, 361 and 367;
- C. Denen Dora Member, covering DD-1 (except those localities which also span SH-4), DD-2 and DD-3, including localities: 58, 116, 118, 121, 133, 134, 161, 162, 167, 168, 169, 171, 172, 174, 182, 184, 185, 187, 188, 190, 191, 194, 195, 201, 220, 233, 239, 241, 246, 247, 250, 259, 260, 287, 291, 296, 307, 309, 315, 316, 317, 321, 325, 332, 337, 342, 344, 358, 362, 378, 379 and 385;
- B. Upper Sidi Hakoma Member, embracing the localities within SH-3, together with those which span SH-4 and DD-1; includes localities: 53, 214, 226, 264, 266, 319, 330, 345, 347, 348, 380 and 384;
- A. Lower Sidi Hakoma Member, comprising localities assigned to SHT, SH-1, SH-2 and SH-3, together with those spanning both SH-3 and SH-4; includes localities: 107, 108, 109, 124, 125, 126, 127, 128, 129, 130, 131, 137, 138, 141, 142, 145, 147, 148, 165, 166, 175, 198, 199, 200, 204, 208, 217, 218, 222, 224, 225, 229, 232, 235, 248, 251, 252, 254, 255, 257, 263, 277, 327, 353, 360, 365 and 374.

There are at present no suids from the Upper Kada Hadar.

Much of the material is housed in the Ethiopian National Museum in Addis Ababa and the author is indebted to the Director, Ato Mamo, for allowing him

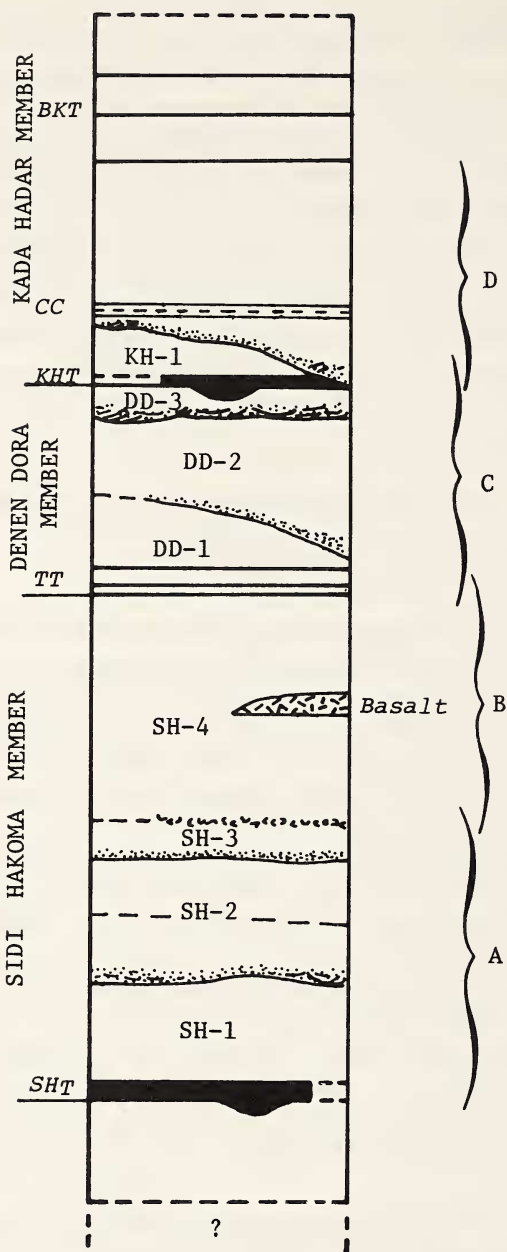


Fig. 1. Stratigraphic distribution of sites that have yielded suid fossil material from the Hadar area.

to work there, and to Ato Woldesenbet for considerable help in handling the material. Thanks are also due to Maurice Taieb, Yves Coppens and Don Johanson for inviting the author to study the suids from Hadar, and to Tom Gray for providing background data and invaluable help with the text. Support funds have been provided by the National Research Council of Canada, the Wenner-Gren Foundation for Anthropological Research, and the International Afar Research Expedition (IARE) and are gratefully acknowledged. A substantial debt is also due to Mr. Richard Wilding of the Archaeology Unit, University of Addis Ababa, for much help, advice and hospitality.

DESCRIPTION

Genus NYANZACHOERUS Leakey 1958

TYPE SPECIES: *Nyanzachoerus kanamensis* Leakey 1958

REVISED DIAGNOSIS: See Cooke and Ewer, 1972

Nyanzachoerus pattersoni Cooke and Ewer 1972

Material

BASAL MEMBER. Mandibular fragment with LM₂₋₃, AL 272-1.

LOWER SIDI HAKOMA. Almost complete skull with associated atlas vertebra, presumed male, AL 137-4 (SH-2); slightly damaged skull, presumed female, AL 107-13 (SH-3); incomplete skull, teeth broken, AL 235-2 (SH-2); palate and part maxilla with cheek teeth, except RP², AL 145-26 (SH-2); palate and part maxilla with partial dentition, AL 235-10 (SH-2); four maxilla fragments with two or more cheek teeth; four single upper teeth; good upper canine, AL 131-8 (SH-2). Damaged mandible with most of the teeth, AL 218-2 (SH-1/3); mandible with damaged symphysis, AL 126-8 (SH-2); symphysis and both mandibular rami with P₃-M₂ on both sides, LM₃ erupting, AL 365-9 (SH-3); left and right mandibular rami with complete cheek teeth AL 137-5 (SH-2); symphysis and left mandibular ramus with teeth, AL 127-15, AL 127-7 (SH-2); right mandibular ramus with RP₄-M₃, AL 165-14 (SH-2); four partial mandibles with several teeth, AL 142-13 (SH-2), AL 137-16 (SH-2), AL 126-65 (SH-2), AL 166-5 (SH-2); six mandibular fragments with two or more teeth, from SH-1 to SH-3, and one from SH-3/4; six mandibular fragments with single teeth; seven single lower teeth and two fragments.

UPPER SIDI HAKOMA. Partial skull with RP³-M³, AL 347-8 (SH-4); parts of broken skull with LM¹⁻³, AL 384-7 (SH-4); RM₃, incompletely erupted, AL 325-3 (SH-4).

DENEN DORA. Maxilla fragment with LM³, AL 134-14 (DD-2/3); isolated RM₁, AL 201-1A (DD-2).

Description

Nyanzachoerus is well represented in the collections up to the end of 1975, with approximately fifty cranial and mandibular specimens and a small amount of postcranial material, although the association is uncertain. The sample is larger than that from Kanapoi in northwestern Kenya, but matches very well in all respects. The two best skulls, AL 107-13 and AL 137-4, agree very closely with the female type and male paratype from Kanapoi, and both amplify and amend the interpretation of those specimens. They thus warrant individual description.

AL 137-4

This skull is very well preserved and has suffered only minor damage (Plate 1). The atlas vertebra is associated with the skull. The tip of the premaxilla and the tips of the nasals are missing. The top of the skull and most of the nasal area are intact, but both zygomatic arches have been damaged. The occiput is complete but there is damage to the auditory bulla and the ear region on the left side. The left upper canine is intact and the right upper canine is broken off at the alveolar margin. Both upper second premolars are broken off and the left dentition is damaged from the back of M¹ to the middle of M³. On the right side P³ is slightly damaged, as is M², but the dentition is reasonably complete. The dimensions and morphology of the skull agree almost perfectly with the paratype from Kanapoi wherever there are corresponding parts. The dimensions of the teeth match well with those of the male, and, as at Kanapoi, are somewhat more robust than the teeth of the female. They are less worn than the teeth of the paratype. Although the zygomatic arches in the Hadar specimen are broken, their roots are present sufficiently to show that the zygomatic arch flared out and was certainly as large as in the Kanapoi specimen. Comparative measurements are given in Table 1.

Of particular value in the Hadar specimen is the excellent preservation of the occipital and back of the cranial region of the skull, which were detached or missing in the Kanapoi paratype. In the Kanapoi specimen there was a part of the fronto-parietal area preserved and it is now clear that the restoration made by Cooke and Ewer (1972) is incorrect, as the skull is longer than had been expected. The parietal area is broad behind the orbits and is still broad at the constriction, about three-quarters of the way to the lambdoid crest. The occiput itself is long and the angle formed between the occiput and the parietal surface is only about 45°. In consequence, the occipital condyles do not lie very far behind

TABLE 1

Measurements of Skulls of *Nyanzachoerus pattersoni* (in mm)

	<i>Hadar Specimens</i>		<i>Kanapoi Specimens</i>	
	AL 137-4	AL 107-13	KP 239 Holotype	KP 264 Paratype
Vertex length	580+(633e)	+457(530e)	510e	620e
Basilar length	447+(490e)	+364(440e)	425	500e
Bizygomatic breadth	+270+	308	c270	c480
Frontal breadth	166	147e		
Parietal constriction	98	72.5	—	76
Crest breadth	155	108e		
Binaural breadth	202	180e		
Greatest breadth across nasals	62	—	53	71
Breadth of muzzle between infraorbital foramina	56e	—	48	66
Palatal length	320+(353e)	+230(305e)	301	352
Breadth of palate				
— between M ³ -M ³	43.0	35.0	33.0	40.0
— between P ² -P ²	71.5	40.2	52.5	73.0
Premaxilla breadth over I ³ -I ³	76e	—	69	95
Diastema I ³ -P ²		—	72	101
Diastema C-P ²	49	—	39.5	c35.0
Length of premolar series	56.5	50.3	51.9	68.0
Length of molar series	105.5	92.0e	95.2	99.1
Length of P ² -M ³	162.0	142.0e	147.0	161.6

e = estimated measurement; c = approximate measurement

the orbits when the skull is resting on the occlusal plane. The distance from the lambdoid crest to the condyles is not much less than the distance from the condyles to the back of M³. The specimen is a little crushed and it is possible that this sharp angle of the occiput is exaggerated by deformation, but even if that is true, the angle of slope is unusually sharp. The back of the occiput is fairly deeply scooped, much as in *Sus* and there is no sign of any median vertical rib. The upper part of the occiput is relatively flat and the wings do not sweep backwards as sharply as in *Sus*, but rather more like the condition in *Hylochoerus*. The ear region is notably wider than the rather narrow occiput, and the auditory canal emerges at an angle of approximately 45° from the horizontal. The bullae have been eroded away but the right paroccipital process is present and stout. The top of the braincase is depressed, and this was regarded

initially as an artifact. However, it has been noted in several skulls and may be a real feature of the genus.

The canine flanges are more or less intermediate in form between those of *Sus* and *Hylochoerus*. There is slight expansion of the nasals just behind the canine flanges, or, more correctly, above the back of the canine flanges, and there are slight signs of rugosity in this area reminiscent of the condition in the bush pig. The upper canine emerges practically parallel to the palatal plane, but sweeps outwards and upwards at the tip. It is truncated along much of the front face by a vertical wear facet. A broad ventral band of enamel occurs and is slightly striated parallel to the length, but not deeply grooved. There is also a posterior narrow inset enamel band but no indication of such a band on the upper anterior face. In cross-section, the canine is almost equidimensional with a squarish U-shape or broad heart shape with a shallow dorsal groove. Considering the massive size of the skull, the canines are relatively small. The cheek teeth conform to the pattern seen in the Kanapoi material except that the enamel is a little more complicated in P³ and P⁴. The upper left M¹ is worn to a flat surface of dentine, but the right one still has a perimeter ring of enamel. The enamel in the upper M² and upper M³ is thicker than it is in the female, corresponding again with features noted in the paratype material. The palatine notch lies only very slightly behind the back of M³ and is broadly rounded, although in some respects a little like a gothic arch. The basioccipital is fairly short, and the basisphenoid descends from it at a steep angle.

AL 107-13

This skull is well preserved, although the superficial bone is in a bad state. In size and morphology it is virtually a twin to the holotype from Kanapoi (Table 1). Most fortunately, it has preserved portions of the skull which were missing in the holotype (Plate 2 A/B). As in the holotype, the palate and cheek teeth are perfectly preserved, although the anterior premolars are missing in the Hadar specimen. The premaxilla, well preserved in the holotype, is missing from AL 107-13. The basicranial region, well preserved in the holotype, is badly damaged and only part of one occipital condyle remains in the Hadar specimen. The right side of the zygoma is missing, but the left zygoma is in excellent preservation. It differs from the type only in that the inflated marginal knob is better developed, and thus the front part of the zygoma projects more at right angles to the axis of the skull. The extra inflation is on the anterior external part of the knob, making it more like that of *Hylochoerus* and adding considerably to the broad platy area below and anterior to the orbit. In the holotype the whole of the upper surface, including the upper part of the occiput, the whole of

the top of the braincase and orbits, and the entire nasal region were missing. These are intact in the Hadar specimen and show that the nasal region was rather narrow, with the nasal bones up-arched; there is some lateral crushing and it is possible that the arching in the specimen may thus be exaggerated.

The parietal is moderately broad and the constriction between it and the lambdoid crest is wide. As in the male specimen, the braincase is hollowed and this increases the probability that this is the natural condition, somewhat resembling the braincase of *Hylochoerus*. Again as in the male, the upper part of the occiput is not deeply scooped, resembling that of *Sus* in general morphology, but the angle between the upper part of the occipital and the parietal surface is abnormally sharp. The rim of the orbits is raised a little above the level of the parietal, recalling the condition seen both in *Hylochoerus* and in *Phacochoerus*. From these raised orbits ridges extend down to at least the end of the lacrimals. The condition of the bone unfortunately makes it impossible to see the lacrimal sutures properly. Although the tip of the snout is missing, it would seem that the narrowest part of the maxillary area is in the vicinity of the infraorbital foramina, and the nasals widen anteriorly and tend to overhang the maxilla. The canine flanges are very similar to those in a male *Sus*. In the Hadar fossil the canine flanges are much more strongly developed than they were in the Kanapoi type.

The cheek teeth are slightly less worn than those of the holotype, but all the features are essentially similar. A minor difference is that in the holotype P³ the tip of the main cone is worn flat parallel to the grinding surface, whereas in the Hadar specimen the wear island runs obliquely from the tip back towards the P⁴. The P³ and P⁴ are also a little stouter and the anterior cingulum is not as strongly developed. The palate is a little wider at the positions of the second upper pre-molars. Essentially, therefore, the only difference between this specimen and the holotype is in the stronger inflation of the zygomatic arches. The bizygomatic width is consequently also a little greater. Both this skull and the male skull show that original estimates of the vertex length were too low, and the skulls are actually a little longer than was indicated in the publication by Cooke and Ewer (1972).

Upper dentition

No specimen occurs in which the upper incisors are preserved, so these teeth are still known only from the Kanapoi holotype.

The upper canine in the male skull AL 137-4 has already been described above. There are a few fragments of other upper canines and one almost complete left upper canine, AL 131-8, and the matching tip of the right canine,

AL 131-7. The canine in the skull measures 40.5 mm (vertical) by 38.8 mm (antero-posterior), whereas the isolated specimen is only 31.9 by 29.0 mm and has a length (in a straight line across the arc) of 130 mm. Although smaller than the male tusk, it is morphologically similar, with a broad ventral band of

Nyanzachoerus pattersoni

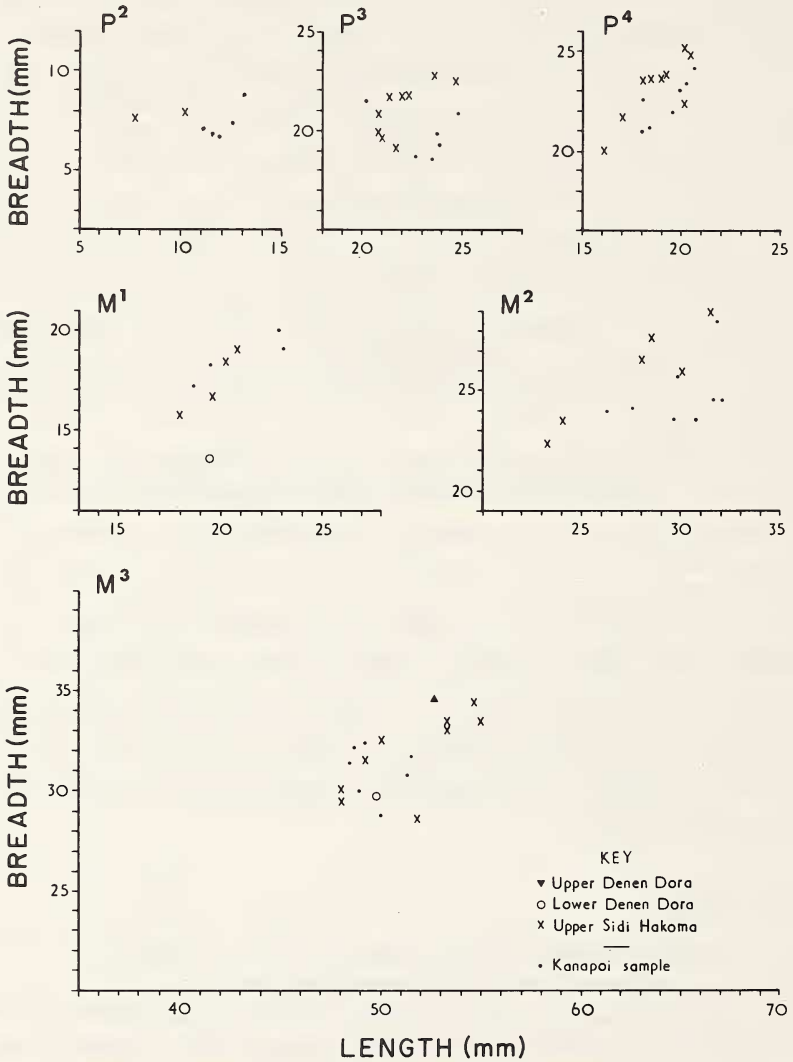


Fig. 2. *Nyanzachoerus pattersoni*. Length-breadth measurements on upper cheek teeth.

grooved enamel and a narrow inset posterior band. However, in this specimen there are traces of an anterior inset band as in typical *Sus*. The tooth is obliquely truncated by a long and slightly wavy wear facet.

Only two specimens of P² are known, and they are slightly smaller than in the Kanapoi material. P³ and P⁴ are well represented and their morphology and dimensions agree closely with the Kanapoi specimens. The same is true also for the molars, as will be seen from the plots in Fig. 2. A few of the upper third molars from Hadar are a little larger than those from Kanapoi, but the difference does not seem to be significant. The upper cheek teeth of AL 137-4 are shown in Plate 2 C.

Mandible and lower dentition

There are several good lower jaws that warrant particular description; all are from the Lower Sidi Hakoma unit. The most complete is AL 218-2, which corresponds in general with that of the paratype from Kanapoi, but is not quite as massive (Plate 3 A/B). It compares very well with the specimen KNM-KP 219, illustrated in Plate 4 of Cooke and Ewer (1972). However, it is more complete in that the entire symphysis is preserved with the two canines broken off a little way above their bases. The four central lower incisors are present, in very advanced wear, and the broken roots of the lateral incisors are also preserved. The anterior premolars are lost on both sides and there is some damage to the teeth, which are in advanced wear. There are no significant differences in the cheek teeth as compared with the Kanapoi material. The incisors are somewhat curious in that they are heavily covered in cement and show a ring of enamel surrounding a core of dentine. The same condition is observed in the incisor teeth of *Notochoerus* and suggests a link between these two genera. The symphysis is not wide but the incisors are arranged in a shallow arc. There is only a small gap between the lateral incisor and the canine but there is a long diastema between the back of the canine and P₂. In cross-section the canines have a blunted V-shape, which is almost heart-shaped. They emerge from the symphysis at a very shallow angle. The symphysis itself is long, with the lower junction level with the back of P₂. The ascending ramus is broken off and the back of the mandible seems very narrow for the massive jaw.

AL 126-8 is an excellent match for the holotype mandible in size, including the presence of the bases of rather small canines. The incisor area has been broken away and cannot be seen. The cheek teeth are well preserved on both sides and in fairly early wear (Plate 2 D). Both lower P₂'s are lost. The lower P₃'s have only the tips in wear and show a remarkably smooth anterior ridge with a distinct backward slope so that the tip of the crown lies over the rear

roots. The broken canine has a flat rear surface and is U-shaped rather than V-shaped, with enamel on all but the posterior surface.

AL 127-15 consists of a complete symphysis with the right P_2 and the whole of the left ramus with all the cheek teeth, while AL 127-7 is the matching right lower third molar in a fragment of mandible. The specimen is in excellent preservation and shows the symphysis extremely well. This is slightly larger than in the holotype mandible and the canines are already somewhat larger than in the previous specimen. The teeth are in early wear and it is possible that this dentition belongs to a young male, although it is not nearly as massive as the other specimen ascribed to a male. Five of the incisors are preserved. The two central incisors are smaller than the second incisors, as was the case with the holotype. The left I_3 is missing, but the right I_3 is present and is a very small tooth, relatively smaller than in the holotype. The central incisors have a strong median ridge on the upper surface and this is flanked by shallow grooves. The second incisors have a strong ridge on the outer side of the midline and the surface from the ridge to the medial side is a gentle slope, whereas on the outer side there is a decided groove. The canines are of moderate size and U-shaped in cross-section. They emerge at a strongly lateral angle, rising only gently above the horizontal plane. The cheek teeth are in early wear. P_2 is small and rather equidimensional. P_3 has the tip only just in wear and the peak lies above the center of the posterior roots. There are no other distinctive features which differ from previous material.

The lower cheek teeth are all well represented and the lengths and breadths of those complete enough to be measured are shown in Figure 3. The dimensions are closely comparable with the Kanapoi sample, although the third molars are, on the average, a little longer.

Discussion

The Hadar material increases very substantially the size of the sample of *Nyanzachoerus pattersoni* and adds to knowledge of some features of the species, especially in providing better evidence for the length of the skull and morphology of the dorsal surface. Although the third molars are slightly longer in the Hadar sample, this cannot be regarded as an indication of evolutionary or temporal trends. The combined Kanapoi-Hadar sample consistently displays a lower third premolar that is shorter and stouter than in the type of *N. kanamensis*, and M_1 is also notably longer in the latter species. In the Kanapoi sample the diastema between the lower canine and P_2 was only about 48-50 mm, compared with 67.5 mm in the type of *N. kanamensis*. In the Hadar sample, three of the lower jaws have diastemata in the range 62-64 mm, although others approxi-

Nyanzachoerus pattersoni

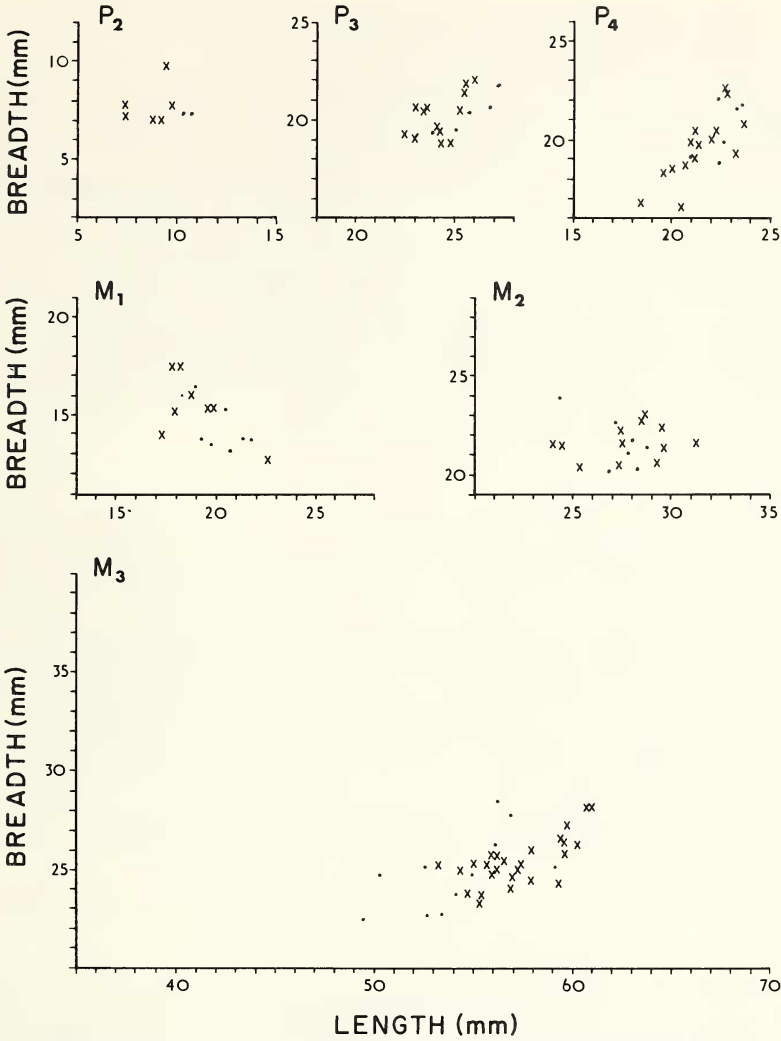


Fig. 3. *Nyanzachoerus pattersoni*. Length-breadth measurements on lower cheek teeth. Key as in Fig. 2.

mate the Kanapoi range. This diminishes the difference but until the elongate, narrow P₃ of the Kanam type can be matched, it seems preferable not to synonymize the two species.

Genus NOTOCHOERUS Broom 1925

SYNONYMY: *Gerontochoerus* Leakey 1943

TYPE SPECIES: *Notochoerus capensis* Broom 1925

NEW DIAGNOSIS: A genus of Suidae of large size, possessing hypsodont third molars in which the main lateral pillars are strongly folded, tending to produce dumbbell or H-shaped enamel islands, particularly in the lowers. Premolars reduced, with only the third and fourth premolars normally retained in the adult. P⁴ with small, closely appressed, paracone and metacone that are well separated from a small rounded protocone. Zygomatic arches robust and possessing thimble-shaped lateral projections in the male. Upper canines dorso-ventrally flattened, carrying a ventral enamel band, and flaring outwards in a strong flat curve not much above the palatal plane. Mandible robust with long, wide symphysis; anterior border almost straight and incisors small and well separated. Lower canines heart-shaped to U-shaped, at least in early stages of growth, and flaring laterally parallel to the uppers.

Remarks

The genotype species was founded by Broom (1925) on an isolated upper right third molar from the Vaal River gravels, South Africa. The tooth lacks an unknown amount from the anterior and was restored by Broom with an additional pair of laterals, making a total of five pairs (the last rather small) and six medians. The main lateral pillars have elongate, flattened outer walls and those on the lingual side are stouter and more complex than those on the buccal side, which are also displaced a little towards the front of the tooth. The tooth is moderately hypsodont, with the crown height more than one and a half times the maximum basal breadth. *Notochoerus eutilus* differs from *N. capensis* in having fewer pairs of laterals and a lesser degree of hypsodonty.

Notochoerus eutilus (Hopwood, 1926)

- 1926 *Hylochoerus eutilus* Hopwood: 21; text-fig. 7; pl. 2, figs. 7-10.
 1942 *Hylochoerus eutilus* Hopwood; Dietrich: 108; pl. 17, figs. 114-126, 128, 130-136; pl. 18, fig. 149.
 1958 *Notochoerus eutilus* (Hopwood) (*partim*); Leakey: 31.
 1958 NON *Notochoerus* (*Gerontochoerus*) *eutilus* (Hopwood); Ewer: 357; text-fig. 11; pl. 4C, 5, 6.
 1970 *Notochoerus eutilus* (Hopwood); Cooke and Coryndon: 147; text-figs. 11, 12; pl. 7, A-E.

Emended diagnosis

A *Notochoerus* considerably bigger than the extant *Hylochoerus*. Upper third molars normally with three or four pairs of lateral pillars, lower third molars normally with four pairs of lateral pillars, plus a small terminal pillar or complex. Successive pairs of laterals separated by single strong median pillars; lateral pillars well separated from each other for most of their height, producing deep lateral valleys between them; cement well developed. Pillars strongly folded near the tips, producing stellate enamel islands in early wear; outer borders of lateral pillars rather flat and longer than the median lobe. Second molars much expanded antero-posteriorly above the base, somewhat as in *Phacochoerus*. Cheek teeth only moderately hypsodont, with maximum crown height in unworn upper third molars normally less than 1.3 times anterior basal breadth and in unworn lower third molars less than 1.5 times anterior basal breadth.

Material

Approximately 150 specimens represent substantial parts of skulls and mandibles, fragments, or isolated teeth that are measurable and there are also some 50 partial teeth. Listed below is a selection of the more important specimens in the collection.

LOWER SIDI HAKOMA. Damaged skull with RM^{1-3} , LM^3 , part LM^2 , AL 108-3 (SH-2/3); palate with P^3-M^3 both sides, AL 127-46 (SH-1/2); pair of mandibular rami with LP_4-M_3 , RM_{2-3} , broken RP_4 , RM_1 , AL 108-2 (SH-2/3); right mandibular ramus with RP_3-M_3 , AL 127-13 (SH-2); right mandibular ramus with RP_4-M_3 , AL 126-64 (SH-2).

UPPER SIDI HAKOMA. Two halves of palate with LP^3-M^3 , RP^3-M^2 , and left mandibular ramus with LP_3-M_3 , young adult, AL 53-44 (SH-3); damaged skull with LP^4-M^3 , RP^4-M^3 , snout lost, AL 171-1 (SH-3); left mandible with LP_3-M_3 (advanced wear), AL 58-13 (SH-4/DD-2).

DENEN DORA. (DD-2): Fine skull, occiput slightly damaged, with P^3-M^3 , both sides, AL 172-1; skull, damaged at occiput and lacking front of snout, and associated mandibles, lacking ascending rami, AL 342-9; damaged skull, lacking snout but with most cheek teeth, AL 167-15; maxilla with LP^3-M^3 and fragment with RM^3 , AL 158-28/29; left maxilla with LP^3-M^3 , and right maxilla with RP^3-M^3 (advanced wear), AL 330-1; damaged mandible with most cheek teeth, AL 174-2; mandible with symphysis, parts of canines and most cheek teeth, AL 174-4; damaged mandible with symphysis and incisors, AL 153-9; partial mandible with incisor sockets, LP_4-M_3 , RM_{2-3} , AL 168-2; (DD-2/3):

Left and right mandibular rami with LP_3-M_3 , RP_4-M_2 , AL 158-34; (*DD-3*): Partial skull, most teeth broken, AL 241-5; palate with P^3-M^3 , both sides AL 116-93; maxilla fragments with LP^{3-4} , LM^{2-3} , RM^3 , AL 116-54; fine mandible, almost complete AL 116-28 (may belong with AL 116-54); broken mandible with nearly all the teeth, AL 168-12; pair of mandibular rami with P_3-M_3 both sides, cracked, AL 185-4; right mandibular ramus with RP_3-M_3 , AL 174-1; broken mandible with LP_3-M_3 , RP_3-M_2 , partial RM_3 , AL 185-3; mandible, damaged anteriorly, with LM_1-M_3 , RP_4-M_3 , AL 378-1; damaged mandible with both canines, LP_{3-4} , LM_3 , RP_4-M_3 , AL 157-3; anterior palate with RP^{3-4} , AL 317-3A.

KADA HADAR. Damaged mandible with LM_{2-3} , RM_{2-3} , other teeth broken, AL 164-2 (KH-1).

Description

Notochoerus is not well represented in the Sidi Hakoma member but is abundant in the Denen Dora member, from which the best and most complete specimens have come. Although the form and structure of the molars have been known for some time, the present account constitutes the first description of the skull and mandible, and of the entire dentition.

The Skull

There are five good crania in the collection, as well as several less complete specimens or substantial parts of skulls. The most complete, which might be regarded as a sort of informal "type," is AL 172-1, from DD-2, which is virtually complete except for damage at the occiput and the loss of the canines and incisors (Plate 4). The vertex length is estimated as close to 580 mm when intact, as compared to about 430 mm in a good adult *Hylochoerus*. One other cranium, AL 108-3, from SH-2/3, appears to be roughly comparable in size, but the other three good specimens are more robust and have an estimated vertex length of approximately 610-620 mm. The more important measurements are given in Table 2.

The overall character of the skull is not particularly like any of the living suids, although in a general way it resembles the warthog, but without the exaggerated elevation of the braincase and orbits. There are also resemblances to *Nyanzachoerus pattersoni* and to the Kanapoi material referred to *N. jaegeri* (Coppens, 1971; = *plicatus*, Cooke and Ewer, 1972). The skull table is broad, with the frontal breadth ranging from a minimum of 166 mm in AL 108-3, to an estimated 230 mm in AL 167-15. The upper margins of the orbits are very

TABLE 2

Measurements of Skulls of *Notochoerus euilus* from Hadar (in mm)

	DD-2 AL 172-1	SH-3 171-1	DD-2 342-9	SH-2/3 108-3	DD-2 167-15
Vertex length	542+(580e)	+550(610e)	+440(c620e)	+395	+412+(c620e)
Basilar length	496	+483(510e)	+340(c520)	+320	+340
Bizygomatic breadth	392	—	c380e	166	c230c
Frontal breadth	187	175e	c200e	49	74
Parietal constriction	50e	—	59	135e	178
Crest breadth	—	—	—	192	234
Binaural breadth	183	185	c62e	—	—
Greatest breadth across nasals	57	77	—	—	—
Breadth of muzzle between infraorbital foramina	c65e	70e	c80e	—	—
Canine flange breadth	163.5	—	—	—	—
Palatal length	369	—	c320e	+152	+205
Breadth of palate	—	—	—	—	—
—between M ³ -M ³	46.7	51.5	59.0	46.7	53.7
—between P ³ -P ³	53.1	58.0	79.0e	—	67.3
Premaxilla breadth over I ³ -I ³	50.5	—	—	—	—
Diastema I ¹ -P ³	175	—	—	—	—
Diastema C-P ³	74	—	—	—	—
Length of premolar series	29.8	31.5	—	129e	33.0
Length of molar series	111.6	119.1	—	—	131.7
Length of P ³ -M ³	141.4	150.0	—	—	164.0

slightly elevated above the top of the braincase, which is gently concave between the eyes and flat behind them. Behind the eyes, the temporal crest sweeps rather sharply inwards, not quite as abruptly as in the antero-posteriorly compressed braincase of the warthog, but a little more abruptly than in the bushpig. As in both these suids, the breadth at the occipital crest is wide, unlike the condition in *Sus*. The parietal constriction is narrow and lies far back on the braincase, quite unlike the condition in *Hylochoerus*. The occiput itself is deeply scooped and resembles that of *Potamochoerus porcus*. There is no median ridge (Plate 3 D).

The slight ridges that form above the orbits are continued in front of the eyes as ridges that flank the supraorbital foramina, very much as in *Nyanzachoerus* and also in the forest hog. The nasals are straight and parallel-sided almost to the level of the canines before tapering to their tips. The muzzle is shaped very like that of *Nyanzachoerus*, with the nasals convexly curved and joining the upper edge of the maxillae to form a fairly sharp edge that may overhang the sides of the snout. The maxillae then curve outwards gently to the border of the palate. Anteriorly, the lower part of the maxillae expands progressively to form the sheath that surrounds the canines, in general rather like that of the forest hog. The resemblance to the forest hog lies in the basic shape of the flange, particularly in the form of the dorsal surface, which is broad with a low lateral crest. However, the canine emerges in a less lateral direction, as the alveolar margin is oblique to the axis of the skull instead of almost parallel to it. Anteriorly the palatal part of the flange extends forwards and is continued as an unusual feature in the form of a lateral shelf that borders the front of the snout, including part of the premaxilla. Posteriorly, the flanges curve smoothly into the root of the zygoma, much as in the warthog, with the infraorbital foramina at the junction; however, the flanges do not have the tubular character of those in *Phacochoerus*. On the palatal aspect, the expanded area has much the shape seen in the forest hog but is tapered forwards by the anterior shelf described above; this makes the premaxilla look shorter than is actually the case.

The root of the zygoma begins just behind the infraorbital foramen and curves smoothly outwards very much as in the warthog until it is at an angle of about 45° to the axis of the skull. It then changes direction and commences a second, rather gentle, curve recalling the form seen in a more exaggerated manner in the warthog. This is complicated by the presence of large thimble-shaped lateral protrusions (or knobs) that project from the jugal area and these tend to obscure the fact that the temporal portion of the zygoma is in a normal position; without the "knobs" the zygomatic arch would be much as in a female *Hylochoerus*. These curious and characteristic lateral protrusions are approximately at right angles to the axis of the skull when viewed from the dorsal

aspect, but from the front or back they can be seen to droop down until their rounded tips are close to the palatal plane (see Plates 3 C, 4). The protrusions seem to consist of hollow bone, and when they are broken away, as is usually the case, it is very difficult to be sure whether they existed or not. Consequently, it is not certain whether they occur only in the males, as might be expected; in one of the skulls AL 171-1, the lower border of the right zygomatic arch seems to be intact and it appears as if no knob existed. In all the other skulls, the survival of the outwardly flared bases of the knobs betrays their existence.

As a result of some elevation of the back of the skull, although not nearly to the extent seen in the warthog, the area below the orbits is broad and platelike. In most of the specimens the area where there would normally be the hollow for the origins of the levator rostri muscles is crushed in and seemed to consist of very thin bone with a sinus space below it. However, two of the skulls show that, far from being scooped out for the muscle insertions, this area was inflated in a manner resembling that of the so-called "lacrimal bulla" in the ox. The same feature is shown by specimens from the Omo area and appears to be a diagnostic characteristic. The attachment areas for the depressor rostri muscles are weakly scooped and it must be inferred that *Notochoerus* did not use its snout for rooting.

One of the skulls, AL 108-3, although lacking the whole of the snout and premolars, is important as it belongs to a young adult; the sutures in the lacrimal area are still open and it is possible to examine the shapes of the major bones. The lacrimal is quite narrow and the lacrimal/parietal suture is high up on the eye socket. The orbit has a strong indentation at the antero-lower edge, often also seen in *Sus*, and the lacrimal extends down into this notch. The lacrimal then widens and runs along the upper crest line in an arch and does not apparently come into contact with the nasals until well in front of the nasal-frontal suture. As the skull is broken at the critical point, it is not clear whether the lacrimal ever does come into contact with the nasals or whether it stops short, although the latter interpretation seems the more likely. The lacrimal is thus a rather elongate, somewhat oval-shaped bone, and it does not show any area of depression for the attachment of the narial muscles. The suture between the maxillary and the jugal is very far forward and lies across the bulging area that has already been noted above. The bulge has collapsed because of the thin nature of the bone.

This same skull has the occiput well preserved. The frontal area is flat, as in other specimens, and the parietal is short and narrowed, much as in *Sus*. The parietal constriction is narrow and *Sus*-like, with the braincase expanding below it. The occiput itself is not very high and is relatively wider than in *Sus*,

but not as deeply scooped. The wings do not project diagonally backwards as they do in the modern pig, but spread laterally as in the bushpig and forest hog; there is no median ridge. When the skull is set in the occlusal plane, the occiput is only about 20-25° off the vertical, and the surface of the temporal condyles lies about level with the top of the foramen magnum. The temporal condyles trend almost perpendicular to the axis of the skull and in consequence, the back of the zygoma, where it bends up to the auditory region, is farther behind the orbit than in *Sus*. The occipital condyles are not elevated abnormally above the palatal plane and the general appearance of braincase height in the skull is achieved by a relative increase in the elevation of the orbits, as well as by the height of the zygomatic area of the maxilla. The ear region is also high and wide, though not to the extent seen in the warthog, and the auditory canal points diagonally upwards at a rather steep angle, perhaps as much as 50° from the horizontal.

The basicranium is poorly preserved in most of the specimens. As far as can be seen, the auditory bullae are relatively small and are strongly compressed laterally. They are very narrow and pointed anteriorly and are directed obliquely towards the center of the palatal notch. The mastoid and paramastoid processes are strong and the paramastoids very stout (and probably also long).

The palate has a general resemblance in shape to that of the forest hog, no doubt dictated by the need to accommodate the extremely large canines. The premaxilla is relatively narrower than in the forest hog and resembles to some extent the corresponding region in the warthog. However, the border of the palate curves smoothly into the expanded area in front of the canines and does not show the abrupt change of angle or notch seen in most other suids (Plate 4). Only one pair of incisors was present and there is no trace of sockets for other incisors. The teeth themselves are not known but the sockets indicate that they were relatively smaller than in the forest hog and comparable with those in the warthog. The anterior palatal foramina are of moderate length and are laterally compressed. The canines emerge very much as in forest hog or warthog, but lie very nearly in the palatal plane. Behind this expanded area, the palate narrows gradually to the point where the canine sockets end and the palate is narrowest just in front of the anterior premolar (normally P³). The posterior palatal foramina lie about opposite the midpoint of the third molars and from them the usual blood vessel grooves run forwards, diverging at the level of the canines and then converging again to their termination at the anterior palatal foramina. The palatine notch lies well behind the back of the third molars.

The canines are large and fairly strongly curved, comprising an arc that may be as much as one third of a circle, as is also the case in the male forest hog or warthog. However, their orientation is different as they extend horizontally

almost in the plane of the palate, with only a small rise at the tips. In cross-section they are unusual as the normal suine structure has been distorted by oblique flattening, with the dorso-ventral dimension only about two thirds to three quarters of the antero-posterior one. On the dorsal surface there is a broad shallow groove and on the antero-ventral surface there is a strongly marked groove that lies almost directly below the dorsal one, making the cross-section rather like a figure 8 on its side, with the smaller loop anteriorly. The posterior face is weakly grooved, thus turning the "lazy 8" into a form that can best be likened to an inverted squashed bell shape (see Figure 4). The ventral band is

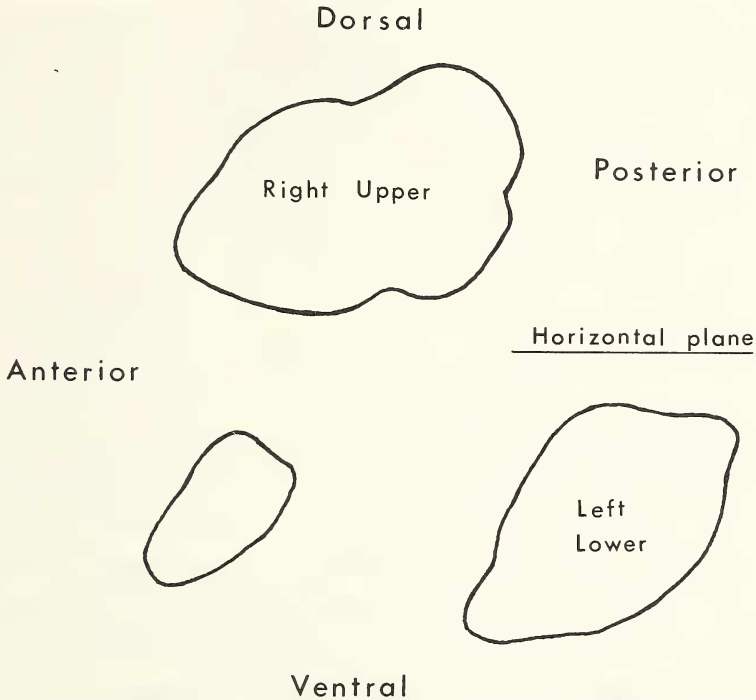


Fig. 4. Outline cross-sections of upper right canine (top) and lower left canines (below) of *Notocherus eutilus*. The top and lower right drawings are taken near the alveolar margin; the lower left drawing is near the tip. Natural size.

made of ribbed enamel and there are narrow inset bands of enamel on the antero-dorsal and postero-dorsal "edges" of the tooth. However, in some specimens the whole tooth is longitudinally ribbed, although only the ventral part has enamel.

In all but one of the skulls and palates, there is no sign of an upper P^2 and no scars that might represent P^1 are found in the fairly long diastema between the canine and P^3 . The same is true of the mandibles and it is clear that only $P^3/3$ and $P^4/4$ are normally retained in the adult. However, AL 342-9 (from DD-1/2) consists of a good skull and associated mandible, a little distorted by oblique pressure, and it is a young adult with the third molars in wear anteriorly but not fully erupted posteriorly. The P_2 is retained on both sides in the lower jaw but the palate is broken across just in front of the upper P^3 's and the presence or absence of P^2 cannot be stated with certainty. If P^2 was present, as seems likely, it must have been separated from P^3 by a gap of at least a few millimetres.

In this skull, AL 342-9, the bone is badly cracked and postmortem distortion has separated the teeth so that the contact facets between them are now from 2 to 8 mm apart (RM^3 has been crushed back into its socket and is 19 mm from the back of RM^2). The P^3 and P^4 in this specimen are in early wear and are fairly typical. P^3 is a subtriangular tooth comprising two external elements (paracone and metacone), lying obliquely to the axis of the tooth row so that the paracone is on the midline. The postero-internal corner is buttressed by a strong oval protocone, separated from the paracone/metacone by a wide and deep fovea, open on the antero-internal side. The back of the fovea is closed by one or two high cingulum cusps. Anteriorly there is a moderately low cingulum band. P^4 is rounded in outline and the crown is about as high as the transverse diameter. The external face shows only the faintest sign of a groove that divides the crown at the tip into paracone and metacone islands. The protocone is rounded and relatively small and is separated from the paracone/metacone by a narrow but well developed transverse valley, closed off posteriorly by a high but thin cingulum. There is a modest anterior cingulum. From the transverse valley, a distinct indentation marks the division between paracone and metacone and there is a matching shallow groove in the protocone, giving a slight + -like form to the valley. In other specimens, the paracone/metacone in P^3 may appear virtually as a single cone. In P^4 the area in the center of the valley may form an isolated pit as advancing wear of the anterior and posterior cingula closes off the valley. There is also a tendency for the three cones to become more columnar in some specimens.

In most of the skulls, even in the young adult AL 342-9, the upper first molar is very worn and the pattern is difficult to discern. It soon becomes a stump of dentine and M^2 moves forward as M^3 erupts behind it, much as is the case with the warthog. In teeth in early wear, M^1 is seen to be formed of two well-developed pairs of laterals, with a single median between them, a weak anterior cingulum complex, and a modest posterior cingulum complex. The

tooth is longest in early wear and becomes almost equidimensional as wear proceeds.

The upper second molar is moderately high crowned and has its maximum length in early wear, when only the tips of the enamel pillars have been abraded. From the base, the anterior face rises forward and the back bulges upward, much as is the case with the more hypsodont second molars of the warthog (Fig. 5). The third molar is initially "tucked in" under the greatly expanded

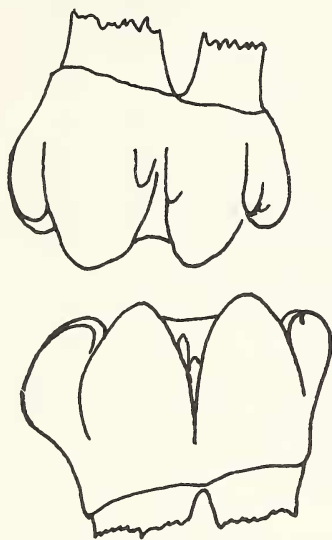


Fig. 5. Sketches to show the lateral aspects of upper (top) and lower (bottom) second molars of *Notocherus euilus*, indicating the substantial posterior bulge of the large cingulum complex. Natural size.

posterior cingulum complex. The crown length thus decreases with advancing wear and the posterior complex shortens, but the second molar remains an elongate tooth even in advanced wear. As far as possible, measurements are taken at the base of the crown so as to facilitate comparison by minimizing changes in the occlusal length with age. The basic structure of the tooth is like that of M^1 but the cingula are better developed, especially the posterior one. The form of the lateral pillars is essentially like the anterior part of the M^3 .

The upper third molars consist essentially of three well-developed pairs of large lateral pillars, followed by a terminal complex that ranges from three small pillars to a good fourth pair, the former being more normal. Very often there is a well-developed fourth lateral pillar on the external (buccal) side but only a small one on the lingual side and the lingual pillars are not level with their

mates but are displaced a little posteriorly. The space between the first and second laterals is wider on the buccal side than on the lingual one. A single median pillar lies between the first and second pairs of laterals, but there may be one or two medians between the second and third pairs. The first and second pairs of laterals are in contact at the midline but the third and fourth pairs may be separated by the partial intervention of the medians. There is an anterior cingulum complex, broken up into several small columns, the center one being almost the size of the medians and forming a wedge between the front pair of laterals. There is usually a stout central terminal pillar at the back of the tooth, but this may sometimes be displaced towards the buccal side and be accompanied by an additional small terminal pillar. In early wear, the lateral pillars show stellate enamel islands, but as wear proceeds, two of the grooves become dominant and divide the pillar into a lateral lobe and a median lobe. The lateral lobe has a relatively smoother outer rim of thicker enamel than is the case in the remainder of the island, although there is sometimes a thin external groove or indentation in the wall of the lateral pillar. The median lobe is less regular and retains some of the stellate appearance by having three or even four "points" initially; but with wear the grooves diminish and the enamel island as a whole becomes progressively more like a dumbbell or H-shape, although minor irregularities may persist on the median lobes, especially in the lingual pillars. The H-shape is best developed at the front of the crown and tends to become distorted in the columns nearer the back, with the median arm of the H displaced forwards. In general, the median area of the H tends to be a little shorter than the lateral one. Minor folds diminish with advancing wear and the pattern becomes very simple. The central, or median, pillars also form stellate enamel islands initially but these become oval or irregularly oval as wear proceeds. Measurements are plotted in Fig. 6 and examples are illustrated in Plates 5 and 6.

Another feature of variation within the Hadar sample is in the degree of upward taper of the crown from the base to the occlusal surface. In general, the occlusal breadth is a good deal less than the maximum breadth of the tooth at the base of the enamel. As the crown height of unworn third molars is not much greater than the anterior basal breadth, the lower crowned variants tend to have a more or less trapezoidal transverse cross-section at the front of the tooth, the broader the base the greater the tendency. In the narrower molars, the sides of the crown are more nearly vertical, although there is always some degree of upward narrowing of the crown. Some individual teeth may resemble the molars of *Nyanzachoerus jaegeri* but are usually distinguishable by the greater development of the talon (*N. jaegeri* has only three pairs of lateral pillars, the third often weak) and by the shape of the enamel islands, which in *N. jaegeri* are more M- or W-shaped than H-shaped. If premolars are present in the

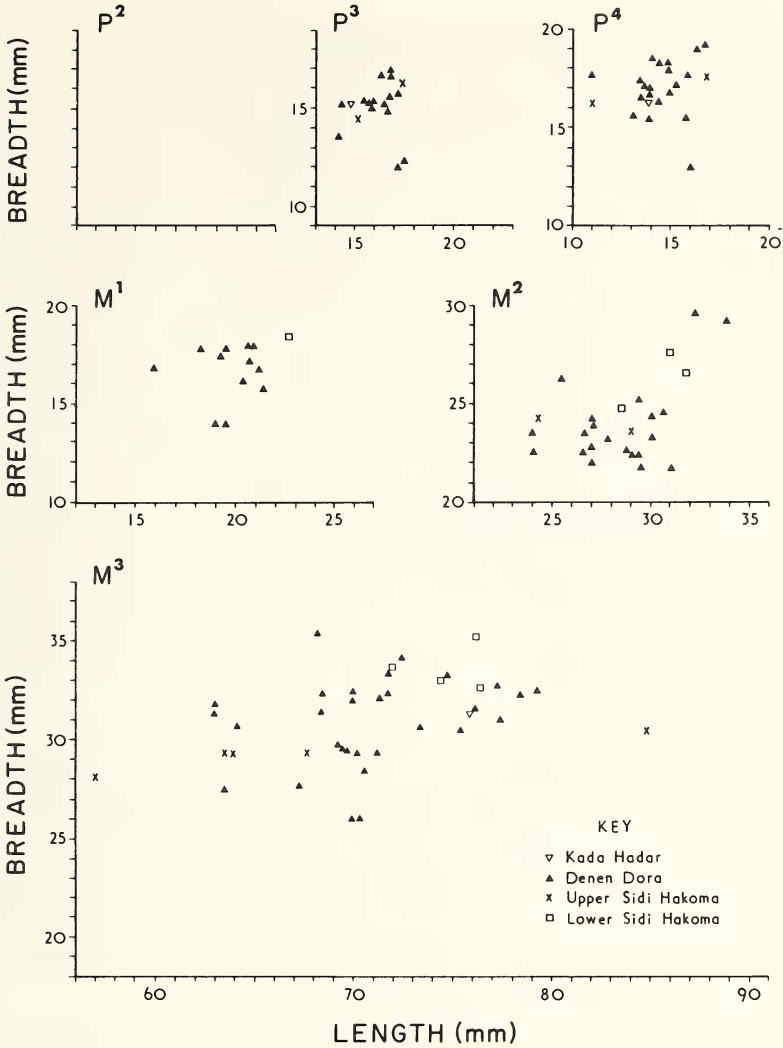
Notochoerus euilus

Fig. 6. *Notochoerus euilus*. Length-breadth measurements on upper cheek teeth.

specimen, the P³ is substantially smaller and P⁴ somewhat smaller in *Notochoerus euilus*. However, the morphological resemblances suggest a close genetic relationship between *N. euilus* and *Nyanzachoerus jaegeri*, and there may be some risk of misidentification in certain isolated specimens.

The Mandible

The lower jaw is represented by several specimens that are reasonably complete except for the invariable loss of the ascending rami. AL 116-28 (from DD-2/3) is probably the best specimen, with the incisors and canines preserved on both sides and a full complement of cheek teeth (Plate 7). The symphysis is long, although there are other specimens that are longer, and it is very wide and spatulate across the canines, very much as in the forest hog. The anterior border is almost straight—even more so than in forest hog—and all six incisors are present (Plate 8 A). They are very much reduced, almost peglike in character, and are strengthened by abundant cementum. The lateral incisor is an absurdly small tooth for a jaw of this size and it looks almost like a first premolar, embedded in a thick shaft of cement. The central incisors are very worn and were probably smaller and shorter initially than those in a modern domestic pig, (the skull of which is only half as large as that of *Notochoerus*); only the bases remain as stumps, about the size and shape of a human incisor and thickly covered with cement. The second incisors are morphologically like shortened *Sus* teeth, of which only the bases remain. Only a few other lower incisors are known, including an RI₁ belonging to the associated skull and mandible AL 342-9 (DD-2) which is a young adult so that the incisor is very little worn. The length of enamel on the anterior (lower) surface is only 14.5 mm and on the upper surface is 22.3 mm along the broad median ridge, while the transverse diameter at the base of the enamel is 8.0 mm and the antero-posterior dimension at this position is 9.3 mm. This is a little more robust than in *Sus scrofa* or *Potamochoerus porcus*, but very much shorter. The median posterior rib is broader and less marked than in *Sus* and the morphology is more like the I₂ than I₁ in the living form. It is more nearly comparable with the corresponding tooth in the forest hog. In this specimen the heavy cement coating is not present, but may have been lost. The whole symphysis in this specimen is very like that of AL 116-28, as also is AL 153-9 (DD-2) in which the broken roots of the four central incisors confirm the small size of these teeth and the two tiny lateral incisors are preserved, with their premolarlike morphology. Ventrally, the symphysis is also rather like that of the forest hog.

In AL 116-28 the canines are intact and emerge from the symphysis at a very low angle, not much above the occlusal plane. They are robust and essentially flattened oval in shape, measuring 42 mm by 27 mm at the alveolar margin, with the long axis antero-posteriorly oriented. The surface is covered with thin enamel, except on a slightly flattened posterior surface. The teeth are fairly sharply curved and carry only a very small anterior wear facet that may be due to use rather than to attrition against the uppers (Plate 8). Other specimens confirm both the form and the attitude of the canines, although in AL 174-4

(DD-2) there is no enamel on the upper face or on the flattened area at the back of the tooth.

In AL 116-28, and in most of the other specimens that include canines, there is a long diastema between the back of the canine and the anterior premolar, which is normally P_3 . This tooth lies just about level with the junction of the two halves of the symphysis. In this specimen there is no trace of P_2 or of a healed scar, despite the excellent state of the bone. The same is true of other specimens, although in most of them the bone is damaged and a scar might easily be missed. However, in the mandible of the young adult, AL 342-9, P_2 is present on both sides. It is a very small tooth, about half the length of the P_3 , and is relatively wide. It consists of a single stout cone with a smooth anterior face, but having a thin ridge running to the back of the crown. The disparity in size between the P_2 and the P_3 is reminiscent of the relationship found in *Nyanzachoerus*. The P_2 is a little stouter than P_2 in *Sus scrofa*, but is of comparable absolute size, whereas P_3 is 50% larger.

The P_3 is represented by a good number of specimens, for which length-breadth plots are given in Figure 7. Also shown are plots for P_3 in *Nyanzachoerus jaegeri* and it will be seen that this tooth is considerably smaller in *Notochoerus euilus*. However, two specimens from the Sidi Hakoma unit are of comparable size. AL 124-5, from the lower Sidi Hakoma, consists only of P_3 and P_4 and its identity is not certain. The other, AL 174-1, comes from the upper Sidi Hakoma, but the third molars are larger than those of *Nyanzachoerus jaegeri* and their morphology is typical for *Notochoerus*, and its length (82 mm) suggests that it is a large *N. euilus*, although this is not certain. Morphologically, the P_3 is moderately elongate and comprises a stout single cone with a smooth anterior face that slopes backwards so that the tip lies over the front of the rear root. There is a well-formed posterior cingulum, half the height of the crown, marked off from the main cone by a weak groove lingually and a stronger one buccally. The P_4 is wider than the P_3 but often slightly shorter, so that it appears almost equidimensional. It also consists of a stout main cone, with the tip practically central, but there is a well-formed, fairly narrow, anterior cingulum and a strong posterior cingulum, or complex, that extends at least three quarters of the height of the crown, much as in *Nyanzachoerus*. In some specimens, especially those in early wear, the tip of the main cone is divided into two elements, the anterior one slightly on the buccal side of the midline, and the posterior one slightly on the lingual side. Because of this slight asymmetry, the posterior cingulum is marked off from the main cone by deep lateral grooves, of which that on the buccal side is the deeper, whereas weaker grooves flank this anterior cingulum and the deeper lies on the lingual side. There is a distinct anterior ridge in most specimens, but it disappears with wear and an anterior cingulum pillar may appear.

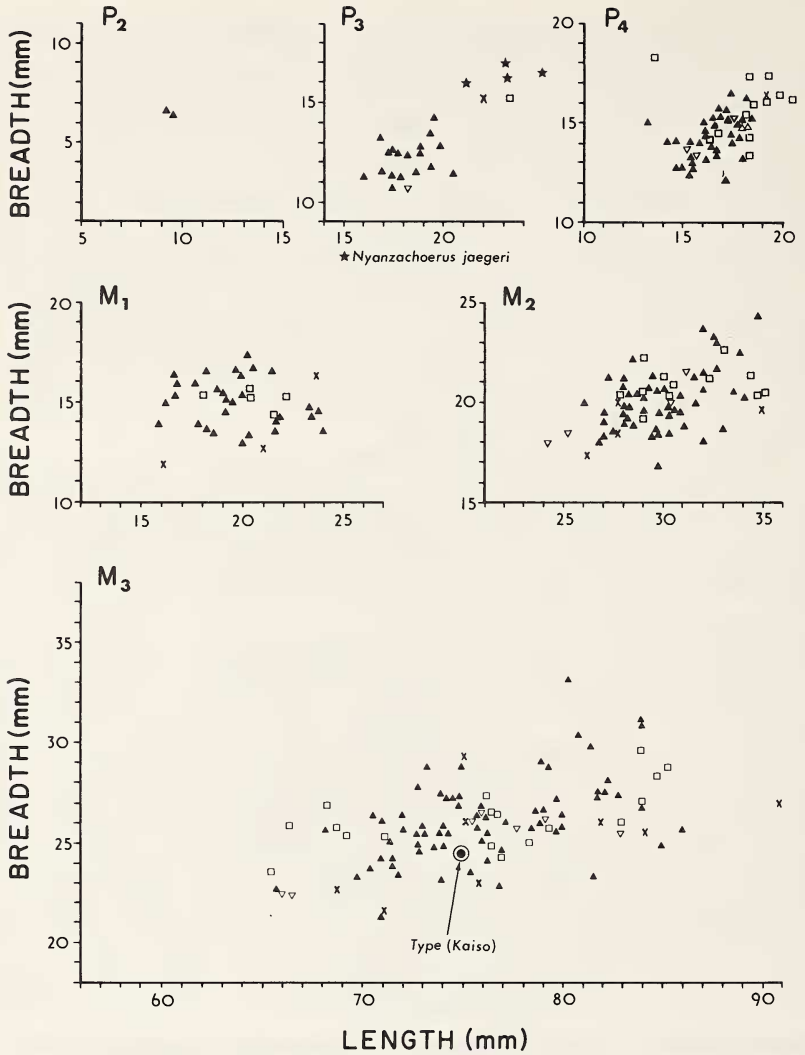
Notochoerus euilus

Fig. 7. *Notochoerus euilus*. Length-breadth measurements on lower cheek teeth. Key as in Figure 6. Data for the P₃ of *Nyanzachoerus jaegeri* and for the Kaiso type of *Notochoerus euilus* are also shown.

The first molar is usually worn to dentine with remnants of enamel but its structure is essentially like that of M₂, except that the posterior cingulum is

weaker. In early wear it is a narrow, elongate tooth, but it broadens and shortens with advancing wear. Dimensions are given in Figure 7.

The M_2 is an elongate tooth with a well-developed posterior cingulum complex comprising a median pillar and two posterior columns that look almost like an incipient third pair of laterals. There is also commonly an accessory basal pillar on the buccal side behind the second external lateral pillar. There is a weak anterior cingulum complex but it is obliterated when the tooth is only half worn. The first paired laterals are usually not quite mirror images, the lingual one being the larger and wearing to an enamel island that may be more X-shaped than H-shaped, while the buccal one sometimes becomes mushroom shaped through lack of the median arm of the H. The second pair of laterals is usually more symmetrical and the islands approximate an H-shape, although the median arm is normally shorter than the lateral one and there is a distinct indentation, or groove, on the median side. The lateral pillars may be angled slightly forwards relative to the base of the crown, when viewed from the side. The anterior and posterior complexes bulge outwards, somewhat in the manner seen in the more hypsodont teeth of the warthog, so the maximum crown length is reached when only about one-fifth of the original height has been worn away (Fig. 5). The anterior complex of M_3 fits under the posterior bulge of M_2 and comes into wear after M_2 has passed its maximum length. The M_3 rotates into position by completion and elevation of the posterior columns and as it grows and abrades, the space between it and the back of P_4 diminishes progressively until the whole of M_3 is in full wear. From a functional viewpoint, the effect is to maintain a reasonably consistent length of molar grinding surface from the young adult, with only the front half of M_3 in wear, to the older adult, with M_1 - M_2 shortened, but the whole of M_3 in use.

The lower third molar normally consists of four well-developed pairs of lateral columns and a terminal complex consisting of three columns, two of which form an incipient fifth pair of laterals; in some specimens these two columns are sufficiently developed to constitute a fifth pair of laterals. Each pair of laterals is well separated from the next pair by wide lateral grooves and by a stout median pillar. As in the uppers, the laterals form moderately stellate enamel islands in early wear, although dominant anterior and posterior clefts soon divide the pillars into external and median lobes. On the first two pairs, an H-shaped enamel island develops with further wear, initially with the two lobes of the island sub equal in size but, as wear proceeds, the lateral lobe may become relatively longer than the median one. On the succeeding pairs, the stellate form persists longer and the H-shape is less obvious. In some teeth, the posterior cleft may dominate so that the shape becomes almost an inverted U. The disparity between basal breadth and occlusal breadth is not as great as in the

uppers, so that the sides of the crown do not taper markedly. The greatest breadth at the base of the crown is often at the second pair of laterals rather than the first. The median pillars form more or less equidimensional enamel islands, initially stellate but becoming oval with wear. The anterior complex is weakly developed. The hypsodonty is moderate with the maximum crown height less than 1.5 times the maximum basal breadth. Length/breadth ratios are plotted in Figure 7 and examples of the lower dentition are shown in Plates 7 and 8.

Discussion

The Hadar collection provides a substantial sample of material that can be ascribed with some confidence to *Notochoerus euilus* as the features of the original syntypes from Kaiso fall well within the range of variation encountered in the Hadar material. If the reconstruction of the holotype RM_3 by Cooke and Coryndon (1970) is approximately correct, it would lie about in the middle of the range observed for M_3 (see Fig. 7). However, those authors considered that material from Laetolil, in Tanzania, differed from the Kaiso species and they referred it tentatively to *Notochoerus* cf. *capensis*. The writer has re-examined this material in East Berlin and, in the light of this study and the variations encountered in the Hadar sample, it is concluded that Dietrich's (1942) original identification as "*Hylochoerus*" *euilus* should stand.

The Hadar sample, although large, comes mainly from the Denen Dora member of the succession and the samples from the other members are rather inadequate for statistical comparisons to be useful. In general, the range for the molars from the Denen Dora would include all the samples from the earlier and later horizons, the only exception being an unusually small M_3 from the upper Sidi Hakoma member. However, for the upper premolars this is less true and there is a suspicion that the specimens from the Sidi Hakoma member may be larger than those from the Denen Dora. From a morphological aspect, the premolars from the Sidi Hakoma are more robust and *Nyanzachoerus*-like than those from the higher members, and there seems to be a change towards higher crowned and more delicate premolars in the upper part of the sequence. The frequency of occurrence of third molars with a strong upward tapering of the crowns also diminishes in the successively higher horizons and the molar structure seems to become more stable and "typical."

From the Usno Formation in the Omo area of southwestern Ethiopia, there is a large sample of material assigned to *Notochoerus euilus* by the present writer but the description is still unpublished, apart from some measurements on the third molars (Cooke, 1976). The range of size variation in the third molars in the Usno sample is almost identical with that for the Hadar material.

However, in the Hadar specimens the enamel is generally thick and does not show the thinning in the folded portions of the lobes that is seen in the Usno material. As a result, the Hadar teeth seem to be less complex in their folding, even in the early stages of wear.

The structural features of the dentition suggest that *Notochoerus* is related to *Nyanzachoerus* and is closest to *N. jaegeri*. The premolars are further reduced in size compared with the latter, but the disparity between P_2 and P_3 remains as evidence for the trend and relationship. The third molars are further enlarged, as compared with *N. jaegeri*, thus increasing the grinding area, but they remain relatively low crowned.

Genus KOLPOCHOERUS E. C. N. and H. E. van Hoepen 1932

SYNONYMY: *Mesochoerus* Shaw and Cooke 1941; *Omochoerus* Arambourg 1942; *Promesochoerus* Leakey 1965; *Ectopotamochoerus* Leakey 1965.

TYPE SPECIES: *Kolpochoerus paiceae* (Broom 1931) (syn. *K. sinuosus* E. C. N. and H. E. van Hoepen 1932).

Diagnosis: Suidae of moderate to large size with skull architecture generally resembling that of *Potamochoerus* in early forms, but zygoma expanded laterally and drooping, especially in the male. Male canines resemble those of *Hylochoerus* in structure and cross-section, but relatively shorter and stouter; female canines much smaller than in the male and primitively rooted in some species. Cheek teeth resemble those of *Sus* or *Potamochoerus* in general structure but molars higher crowned and have lateral columns that are distinct and well separated. Talon of third molar tends to become more developed than in *Sus scrofa* or *Potamochoerus porcus*, exceeding the length of the main body of the crown in advanced species. Molar brachydont or moderately hypsodont, always strongly rooted. Little cement in more brachydont forms, abundant in hypsodont molars. Premolars rather more *Sus*-like than *Potamochoerus*-like; P^2 and P^3 triangular with well-developed protocone; P^4 equidimensional with a strong protocone and tendency toward the development of multituberculate and complex islands; P_4 has elevated anterior and posterior cingulum cusps and a double central cusp with the two elements displaced laterally relative to one another.

Remarks. *Kolpochoerus* is widely distributed in the later Pliocene and Pleistocene, ranging from South Africa to North Africa. This generic name has priority over *Mesochoerus*, which has been used in most of the literature. The type species is one of the most advanced in the genus.

Kolpochoerus afarensis sp. nov.*Diagnosis*

A suine about the size of the living bush pig, recognizable as *Kolpochoerus* by the structure of the zygomatic arch; differing from *Potamochoerus porcus* in possessing premolars that are less reduced and morphologically somewhat intermediate between premolars of bush pig and wild boar; P¹ normally, and P₁ sometimes retained in adult; lower canines verrucose; third molars relatively larger than in bush pig, tending to be more columnar and with smoother enamel on outer faces of main pillars; distinguished from *Kolpochoerus limnetes* by smaller size and by possession of only two pairs of fully developed laterals in the lower third molars.

Holotype. AL 147-10 in the Ethiopian National Museum, Addis Ababa, cranium with occiput and basicranium damaged, zygomatic arches and tips of premaxillae lost, P³-M³ present on both sides in early wear; some lateral distortion and crushing of the cranium.

Locality: Hadar, Ethiopia

Hypodigm: SIDI HAKOMA. Type (SH-2); palate of juvenile with erupting canines, RP¹, RM¹⁻², LM¹⁻² intact, AL 224-3 (SH-1/2); maxilla fragment with RP⁴-M², AL 222-4 (SH-1/3); maxilla fragment with RM²⁻³, AL 218-1 (SH-1/3); isolated RM³, AL 200-13 (?SH-1); isolated RP⁴, AL 165-12 (SH-2). Mandibular ramus with base of canine, LP₄, LM₂₋₃, roots LP₁₋₃, LM₁, AL 109-1 (SH-2); mandibular ramus with roots of LP₃, LM₁ broken, LP₄, LM₂₋₃ intact, AL 127-38 (SH-1); mandibular ramus with LM₂, partial LM₃, broken LP₄-M₂, AL 165-5 (SH-2); mandibular ramus with LM₁₋₃, AL 125-4 (SH-1/2); mandibular fragment with damaged LM₁-LM₃, AL 217-3 (SH-1/3); mandibular fragment with RdP₄-M₂, AL 248-3 (SH-2); mandibular fragment with LM₁₋₂, AL 214-1 (SH-4); mandibular fragment with LM₂₋₃, AL 148-101 (SH-1); mandibular fragments with M₁: AL 147-24 (SH-2), AL 266-3 (SH-3), AL 277-8 (SH-2/3); mandibular fragments with M₃: AL 131-4 (SH-2), AL 229-3 (SH-3), AL 199-2 (?SH-1), AL 251-34 (SHT), AL 255-1 (SH-1/2), AL 165-4 (SH-2), AL 327-19 (?SH-2), AL 325-9 (SH-4), AL 259-2 (SH-2); isolated M³, AL 233-3 (SH-4).

Referred Material: DENEN DORA. Partial cranium, lacking snout and occiput but with zygomatic arches, teeth broken, AL 154-34 (DD-2); pair of maxillae with LP³-M², RP⁴-M², AL 116-1 (DD-3); maxilla fragment with RP³-M¹, AL 118-7 (DD-3); maxilla fragment with LP⁴-M³, AL 385-2B (DD-3); palate with P⁴-M³ both sides and two fragments of mandible with M₂₋₃ both sides, AL 56-16 (?DD-2/3); maxilla fragments: with P⁴-M¹, AL 332-35 (DD-1), AL

358-12 (?DD-2); and M¹⁻², AL 116-114 (DD-2); with M²⁻³, AL 287-2 (DD-1); isolated LP⁴, AL 342-13 (DD-2); isolated M¹, AL 116-42 (DD-2/3); isolated M³, AL 116-7 (DD-2), AL 201-1B (DD-2), AL 220-3 (DD-2). Incomplete mandible with roots of incisors and canine, LP₃-M₃, parts of right ramus with RM₂₋₃, AL 134-7 (DD-2); symphysis with base of left canine, AL 220-2 (DD-2/3); symphysis, right ramus with RM₂₋₃, anterior teeth broken, left mandibular fragment with LM₂₋₃, AL 321-10 (DD-3); mandibular ramus with LP₃-M₃, AL 385-2A (DD-3); mandibular ramus with RP₄-M₃, AL 168-13 (DD-2); symphysis fragment with RI₁, LI₁₋₂, left ramus with LP₂-M₃, part right ramus with RP₂₋₄, AL 186-20 (DD-3); juvenile mandibular ramus with RP₄-M₂, M₃ in crypt, AL 185-20 (DD-3); mandibular fragments with LM₃, RM₁₋₃, AL 116-60 (DD-3); mandibular ramus with RP₄-M₃, AL 116-15 (DD-3); mandibular ramus with RP₄-M₃, AL 183-44 (DD-3); mandibular fragment with LM₁₋₃, AL 169-16 (DD-2); mandibular fragments: with M₂₋₃, AL 379-3 (DD-2/3), AL 118-6 (DD-2/3), AL 291-10B (DD-3); with M₂, AL 302-4 (DD-2), AL 169-19 (DD-2); with M₃, AL 169-18 (DD-2), AL 187-12 (DD-3), AL 309-2 (DD-3).

KADA HADAR. Symphysis with four incisors and both canines, parts of rami with damaged LP₃₋₄, RP₃, roots of RP₄-M₂, damaged RM₃, AL 157-2 (KH-1); mandibular fragment with LP₃-M₃, roots LP₂, AL 359-1 (KH-2); mandible fragment with RdP₄, AL 367-1 (KH-2/3).

HADAR SOUTH. Maxilla fragments with LM²⁻³, RM³, AL 273-1; mandible fragment with RdP₄, RM₁, and erupting RM₂, AL 273-2.

UNCERTAIN HORIZON. Isolated M³, AL 246-5.

Description

The holotype comes from the middle part of the Sidi Hakoma member but unfortunately there are few other specimens of the upper dentition from this stratigraphic unit. The material from the Denen Dora unit seems to be a little larger, but the sample from the Sidi Hakoma is too small for it to be clear whether this is a real trend or a chance variation. The holotype lies near the lower limit for the entire sample but the morphology is characteristic. The samples for the lower dentition are bigger and show only a small trend towards larger size.

The Holotype

The holotype is an incomplete cranium from site AL 147, which also

furnished one isolated lower first molar. The cranium has lost the tip of the snout in front of the third incisors and also the upper part of the occiput, the occipital condyles, much of the auditory bullae and paramastoid processes, and most of the zygomatic arches. The specimen is deformed by pressure from the right side so that the midline of the skull is now almost directly above the left tooth row. In part, this has been accomplished by shearing of the maxilla and translocation of the snout and frontal area with relatively little actual distortion of the facial bones, although there is a mosaic of fracturing. The maxillary root of the right zygoma is partly preserved. There is also some backward compression of the skull. The palate is virtually intact and P³-M³ are present on both sides and almost complete, except for slight damage to RM¹ and LM³. The third molars are still erupting and the main pillars are just coming into wear, so that the dentition is in an almost ideal state. Measurements on the skull are necessarily a little speculative but some are given in Table 3, together with reliable measurements on the cheek teeth. The skull and teeth are illustrated in Plates 9 and 10 A.

TABLE 3

Measurements on Holotype Cranium of *Kolpochoerus afarensis* (in. mm)

		AL 147-10					
	Vertex length	+296 (c340-350e)					
	Nasal breadth	c51					
	Muzzle breadth	c55					
	Ocular breadth	c75					
	Frontal breadth	c110					
	Posterior palatal breadth	33.5					
	Posterior maxillary breadth	80.0					
	Anterior palatal breadth	c4 le					
	<i>length</i>	<i>breadth</i>	<i>height</i>		<i>length</i>	<i>breadth</i>	<i>height</i>
LP ³	14.7	9.8	10.5+	RP ³	14.0	10.0	11.5+
LP ⁴	12.7	13.6	10.0+	RP ⁴	12.8	13.2	9.5+
LM ¹ occlusal	18.6			RM ¹ occlusal	18.2		
basal	15.4	15.2	9.5+	basal	14.9	15.1	7.0+
LM ² occlusal	23.9	12.7		RM ² occlusal	24.1	13.0	
basal	21.0	19.2	12.5+	basal	21.4	19.4	12.5+
LM ³	34.3	20.2	16.0e	RM ³	33.9	19.6	16.0e+

In overall size and general morphology, the holotype cranium is very similar to the corresponding parts of the skull in *Sus scrofa* or *Potamochoerus porcus* and, in the absence of the zygomatic arches, might belong to either

genus. The nasals are moderately wide and appear to have been gently arched and to have curved smoothly into the side walls of the muzzle. The supraorbital foramina are about in line with the front of the orbits, and the canals leading from these are moderately deep. The orbits were well below the frontal surface, which was gently arched, and the frontal breadth is normal. The parietal constriction is narrow, being substantially less than the breadth of the snout, as is common in *Potamochoerus* whereas in *Sus* it is usually wider than the snout. The braincase probably bulged outwards below the parietal crest, as in the bush pig, but it is too crushed for this to be certain. The occiput was apparently narrow, but this area is too badly damaged for details to be seen. However, the squamous temporal bone was clearly broad at the base, with the external auditory meatus fairly low down, as in *Potamochoerus porcus*, not narrow and rather high as in *Sus scrofa*. The infraorbital foramina lie above the junction between P⁴ and M¹; in *Sus scrofa* they are normally above P⁴ and in *Potamochoerus porcus* above M¹. The maxillary root of the zygoma has been pushed back into the orbit, but it would seem that there was only a moderately scooped area for the levator rostri attachments, not as deep as in typical *Sus*. The remnants of the auditory bullae and the paramastoid process appear normal.

The front of the premaxilla is broken through the sockets of the second left and third right incisors, but it is clear that the front of the snout was moderately long and narrow, much as in *Sus scrofa*. The left canine has been broken off with part of the bone, but the form of the flange is clearly seen and is small with an antero-posterior measurement of 15.3 mm and a transverse measurement of 8.9 mm. It is laterally more compressed than in a bush pig of the same age and like that of *Kolpochoerus limnetes*, but smaller. There is a good deal of distortion, but it would seem that the tusk pointed downwards much as in females of the wild boar and did not curve sideways even to the extent seen in modern bush pig females. There is a gap of approximately 10 mm between the front of the canine and the back of the socket for LI³, but crushing makes this measurement unreliable. About 1 cm behind the canine is the front of the anterior root of LP², but it is not possible to determine whether P¹ was present or not, as this area is distorted and damaged. Judging by the roots, P² was about 12 mm long.

Of the cheek teeth, only P³-M³ of both sides are known in the holotype. Measurements are given in Table 3 and length/breadth ratios are plotted in Fig. 8. The dimensions are closely comparable with those of *Sus scrofa*. Compared with *Potamochoerus porcus*, the third molars are larger than is usual, but the other teeth are similar in size. Morphologically, they are somewhat intermediate in character, but are less columnar than in *Kolpochoerus limnetes*.

Kolpochoerus afarensis

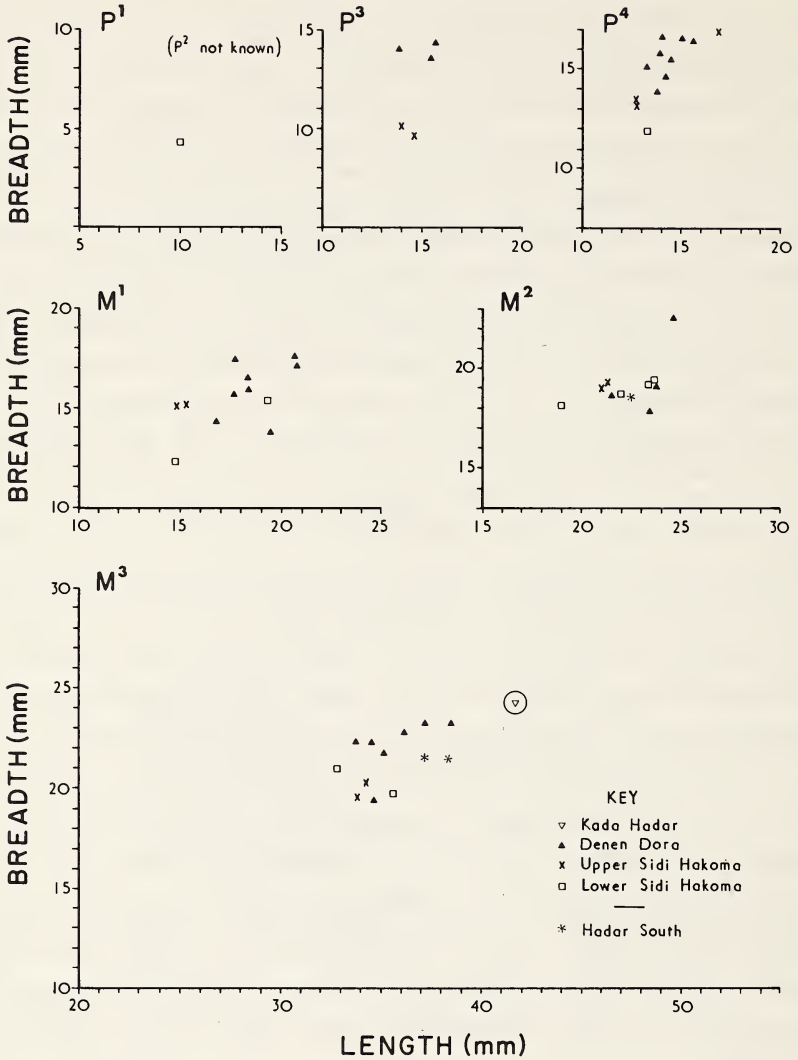


Fig. 8. *Kolpochoerus afarensis*. Length-breadth measurements on upper cheek teeth. The circled measurement is for an unusually large specimen.

P³ is a sub-triangular tooth with the main cone (paracone) developed more strongly than in *Sus scrofa*, but not as robust as in typical bush pig. As in the latter, the anterior cingulum is not very well developed, but is strong enough for

an antero-internal fossa to develop in *Sus*-like fashion, though weaker. The posterior cingulum is also lower than in *Sus* and the postero-internal cusp (metaconule) is small and rather isolated, but does not lead to the formation of a strong fovea in front of it, as is usual in the bush pig. The main cone is linked to the cingulum by well-developed ridges, making the tooth more sectorial than in bush pig at the same dental age. This structure is normal in *Kolpochoerus*.

P⁴ has the two outer main cusps (paracone and metacone) well developed and well separated, as in *Sus scrofa*, and the paracone is also somewhat larger than the metacone, whereas in the bush pig the two cones are roughly equal in size and are closer together. The protocone is large and antero-posteriorly elongate, and lacks any trace of the median spur that occurs typically in *Sus scrofa*, but not normally in the bush pig. In the former a wide and persistent fossa separates the paracone/metacone ridge from the protocone, but a narrow spur from the back part of the paracone juts into the fossa and tends to form two foveae, of which the anterior one is open to the front as the anterior cingulum does not block it. In the bush pig the fossa is narrow but the anterior cingulum extends partly around the protocone and blocks off the anterior fovea, while the posterior fovea is blocked by a strong cingulum that is tied to the back of the paracone. In the fossil, the paracone has a strong median spur that meets the front of the protocone and there are well developed cingulum cusps at the back of the crown that block the fossa. The result is the formation of a deep, wide, conical fovea that looks very like a volcanic crater. The anterior cingulum extends part way around the protocone, as in the bush pig, and a very small fovea is formed between it and the paracone and protocone. The cingulum development has resemblances to the bush pig condition, but the isolated protocone and very large fovea is more like the wide fossa in *Sus scrofa*. The distinctive structure of later *Kolpochoerus* is not yet developed.

M¹ and M² are very similar to the corresponding teeth of the wild boar and of the bush pig, which can be difficult to distinguish from one another. In *Sus scrofa* the enamel is thinner than in *Potamochoerus porcus*, and in the earlier stages of wear the clefts (or furrows of Hünemann, 1968) in the main pillars are wider and more open in *Sus* than in *Potamochoerus*, where they are hairline cracks. In the fossil teeth they conform to the latter rather than to the former. The successive pairs of laterals are more widely spaced than in *Sus scrofa*. The latter also tends to have the space between the first and second lateral columns on the inner (lingual) side filled by well-developed accessory basal pillars, which are less strongly formed in the bush pig. The fossil has only weak basal pillars on the inner side but does possess a single short basal pillar on the external (buccal) side between the well-spaced laterals; this sometimes occurs in second molars both in the wild boar and in the bush pig.

The third molars are relatively larger than in the bush pig but match closely in dimensions with the wild boar. There are two pairs of laterals and a single stout terminal pillar, as in both these living suids, although in both the talon may sometimes be more complex. As was the case with the first and second molars, the main pillars are smoother and less plicate than in *Sus scrofa*, and are also more distinctly separated and columnar than in the wild boar; indeed they are also rather simpler and better separated even than in living *Potamochoerus porcus*, presenting a less crowded appearance to the crown, as might be expected in a very early stage of *Kolpochoerus*.

Other cranial material

AL 224-3, from SH-1/2, is an important specimen as it provides information about the anterior cheek teeth. It is an incomplete palate, with a narrow rim of maxilla, and is broken across in front of the canines and through the palatal notch. The third molars are still completely in the crypt and the deciduous teeth have just been shed. The first and second molars are intact on both sides and the two canines are almost intact. RP^1 is preserved but LP^1 is broken off at the roots and the remaining premolars are represented only by the sockets. The root impressions of the last deciduous tooth on the right side are still visible and the distance from the front of P^1 to the front of M^1 on this side is about 5 mm longer than on the left side, so it may be assumed that the teeth will close up a little. There are no obvious gaps and it is considered that the arrangement was very much like that in *Sus scrofa*, with P^1 slightly separated from the canine, and the premolars just in mutual contact. Each of the P^1 's has a length of 9.8 mm and estimated measurements for the other premolars are approximately 14 mm for P^2 , 15 mm for P^3 and 14 mm for P^4 , an aggregate of 53 mm. The actual distance from the front of LP^1 to the front of LM^1 is 56.0 mm. This is greater than P^1 - P^4 in *Sus scrofa* at the same stage of dental maturity, which ranged from 45 to 48 mm in three specimens available for comparison, but the difference is not great. In *Potamochoerus porcus*, P^1 is normally absent, but it is sometimes present in juveniles and is shed very early in life, at approximately the same time as the last milk tooth. In the fossil it is clear that P^1 is firmly rooted and it is expected that it would remain as a functioning tooth in the adult. In size and morphology it is almost identical with that in the living wild boar. In dimensions, the P^1 corresponds closely to P^2 in the bush pig, but the tooth is narrower and more bladelike in appearance; it is longer than the P^1 occasionally found in the bush pig in young animals. The M^1 and M^2 have the same characters as the corresponding teeth in the holotype cranium, but M^2 lacks the small external basal pillar between the laterals. The canines have only just emerged but the tip is already worn to a small facet about three quarters of a centimetre in length

(Plate 12 A). The anterior and posterior crests typical of a young canine are still visible and the morphology does not differ significantly from that of wild boar or bush pig at this stage of eruption.

The two maxillary fragments, AL 222-4, AL 218-1, and the isolated RM³, AL 200-13, confirm the general characters shown by the molars in the other specimens described above. The isolated RP⁴, AL 165-12, and the RP⁴ in the maxilla AL 222-4, do not exhibit the large craterlike fovea seen in the holotype and the pattern is more like that of the bush pig and early *Kolpochoerus limnetes*.

Mandible

The lower jaw is not very well known from the Sidi Hakoma member. The best specimen is AL 109-1, which is a left mandibular ramus broken through the canine socket, but retaining the left canine (Plate 12 B). The canine is verrucose and thus closer to the characteristic tusk of *Potamochoerus porcus* than to the scrofic one of the wild boar. The posterior face at the alveolar margin measures 15.0 mm, the internal face 19.7 mm, and the external face 17.5 mm. The three anterior premolars are all broken off at the roots, but their sizes can be estimated. P₁ lies about 7.5 mm behind the canine, as in *Sus*, and there is a gap of 25 mm between it and P₂, which must have been approximately 12–13 mm long, while P₃ had a length close to 15 or 15.5 mm. P₁ is thus about the size of the corresponding tooth in *Sus scrofa*, as also are P₂ and P₃. P₁ is about the same size as P₂ in the bush pig and both P₂ and P₃ are larger than in *Potamochoerus porcus*. In the fossil, P₄ is intact and is a little larger than in the bush pig, but close to the wild boar in size. The P₄ in *Sus scrofa* has a strong main cone consisting of two elements that are laterally displaced, so that there is a marked "kink" in the crest; in *Potamochoerus porcus* the protocone is stout and undivided. In the fossil there is a distinct deviation in the crest. The crest is also bladelike, as in *Sus scrofa*, and less expanded than in the bush pig; the internal buttress of later *Kolpochoerus* is not developed. The anterior and posterior cingula, although quite well developed, are not as high as in the wild boar. The tooth is thus more or less intermediate in character. In this jaw, the crown of M₁ is broken away but M₂ and M₃ are preserved. As was the case with the upper molars, they resemble the corresponding teeth of *Sus scrofa* and *Potamochoerus porcus* in structure but the pillars are less complexly folded than in the wild boar and are more columnar and better separated even than in the average bush pig. However, the third molar clearly has only two pairs of laterals and a stout median terminal pillar, flanked by accessory basal pillars, and is thus simpler than the specimen from Kaiso that Cooke and Coryndon (1970) named "*Sus*" *waylandi*, in which there are three pairs of laterals, as in

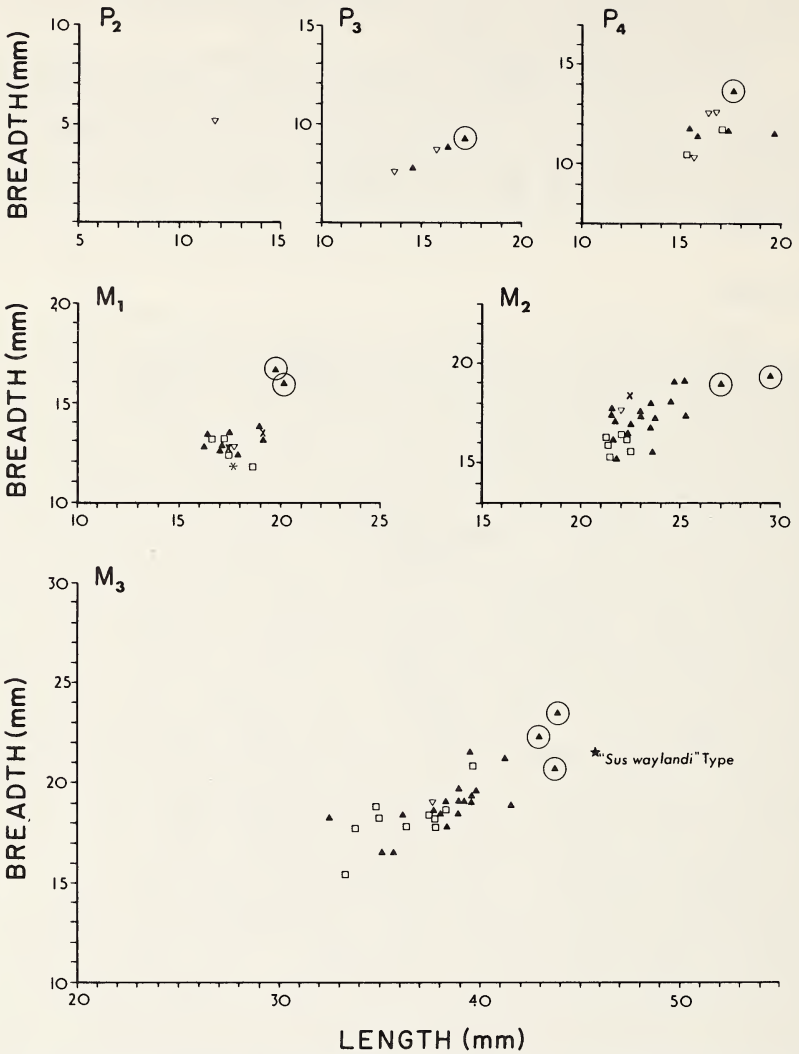
Kolpochoerus afarensis

Fig. 9. *Kolpochoerus afarensis*. Length-breadth measurements on lower cheek teeth. Key as in Figure 8. The type of "*Sus waylandi*" (now placed in *K. limnetes*) is also shown.

typical *Kolpochoerus limnetes* (to which *waylandi* is now referred).

The other mandibular fragments do not add significantly to the information given above, but serve to confirm that AL 109-1 is a fairly representative specimen. Only AL 127-38 has the P₄ preserved, and this is slightly smaller

than in AL 109-1, but morphologically similar. There are ten third molars from the Sidi Hakoma member, and these range in length from 33.5 mm to 39.8 mm, but all have essentially similar morphology. Length/breadth ratios are shown in Fig. 9.

Referred material

The Denen Dora member has yielded a substantial amount of material that can be referred without hesitation to the same species as that occurring in the Sidi Hakoma member. However, there are also found in the Denen Dora member four specimens that seem to be distinctly larger than the rest of the sample and also show slight differences in morphology. Although it is very likely that they are only variants, they will be discussed separately below. It is possible that they represent the beginning of an actual dichotomy. Under the circumstances, it has been thought best to restrict the hypodigm to the Sidi Hakoma sample. Many of the Denen Dora specimens contain parts that were not represented in the Sidi Hakoma material and thus warrant particular description. Length/breadth plots for all the referred cheek teeth are shown in Figs. 8 and 9.

AL 154-34 (DD-1/2) is a partial cranium, lacking the snout, the back of the braincase and basioccipital area, but apparently undistorted and having both zygomatic arches well preserved. It is illustrated in Plate 11. Most unfortunately, the M^2 and M^3 on both sides were in very advanced wear and have been damaged as well, so measurements on these are only approximate. RM^2 has a basal length of close to 23.5 mm and a breadth of 19.0 mm; LM^3 has a basal length of 38.5 mm and a breadth of 22.5, in good agreement with other material in better preservation. Both orbits are preserved and the frontal is broken across the braincase just behind them, so it is possible to measure the frontal breadth as close to 110 mm, which is virtually the same as the estimate for the holotype cranium. The interocular breadth is 85 mm, which is also close to that for the holotype, and the morphology of this part of the snout is very similar. There can be no reasonable doubt about the identity of the specimen as representing the same species as the holotype. The top of the orbit lies approximately 150 mm above the occlusal plane and the front of the orbit lies very slightly in front of the back of M^3 , as is also the case in *Potamochoerus porcus*, whereas in *Sus scrofa* (wild) and *Kolpochoerus limnetes* it is usually slightly behind the back of M^3 . The lateral profile is decidedly steeper than in wild *Sus scrofa*, or even *Sus verrucosus*, and is perhaps a little steeper than in *Potamochoerus porcus*, which it otherwise resembles closely. As in the bush pig, there are elevated ridges flanking the supraorbital canals, clearly seen as bumps in the profile. The flat naso-frontal area overhangs the maxilla, forming

a rather sharp edge above the scooped out area for the levator rostri muscles, as in the bush pig; the scooping is not quite as deep as in the wild boar. The origin of the depressor rostri, however, is relatively weak and shallow, as in *Sus scrofa* and *Kolpochoerus limnetes*, and not as deeply excavated as in the bush pig. The ridge between these two areas, which forms the maxillary root of the zygoma, is only moderately developed and rounded, unlike the strong sharp ridge of *Sus scrofa*. The root of the zygoma curves rapidly outwards until it is perpendicular to the skull axis and the jugal is greatly expanded laterally into large bosses that are rugose over much of the inflated area. Although there is a basic resemblance to the zygoma in old male animals of *Potamochoerus porcus*, there is less of a forward bulge and the lateral expansion is very typical of *Kolpochoerus limnetes*. There is also a resemblance to the zygomatic enlargement in the forest hog, *Hylochoerus meinertzhageni*, but in that species the zygomatic arches droop almost to the occlusal plane, whereas in the fossil and in the bush pig they lie at a much higher level. In the forest hog, the maxillary root of the zygoma is quite different; the broad parietal area is also quite unlike the braincase in the holotype. The bizygomatic breadth is 223 mm, which is greater than is usual in *Potamochoerus porcus*, for which 200 mm is rare and 175–180 mm more normal. The structure of the zygoma, coupled with the other morphological features already discussed, seem to place *afarensis* firmly in the genus *Kolpochoerus*, despite the existence of some more *Sus*-like characters and some *Potamochoerus* resemblances.

The upper dentition is well represented in the referred material, which is listed above, and includes two specimens in which P^3 is preserved, AL 116-1 (Plate 10 B) and AL 118-7 (DD-2/3). Both these P^3 's are more robust than in the holotype and correspondingly a little less like those of *Sus*, but larger than the somewhat reduced P^3 of *Potamochoerus porcus* (Fig. 8). The P^4 's are also larger than in the holotype, but not quite as large as in specimen AL 165-12 from the upper Sidi Hakoma member. The protocone blocks the fossa, as in the bush pig, but the paracone and metacone are more like those in *Sus scrofa* and *Kolpochoerus limnetes*. The third molars are also generally larger than the Sidi Hakoma sample, and there is a tendency for the molars to be more columnar and to have less secondary plication than in wild boar or in bush pig. In particular, the outer lateral pillars tend to become more rounded and smooth walled.

The best mandible is AL 134-7 (DD-2/3), comprising the symphysis and complete left ramus and also a fragment of the right ramus with RM_{2-3} . The canines are broken off at the alveolar margin and the incisors are badly broken. The left side of the jaw is damaged in front of P_3 and it is thus impossible to determine the size or form of P_2 . There is no sign of P_1 , or of a scar where it might have been (Plate 13 A/C). The general shape of the jaw and the sym-

physis are like those of the wild boar and the bush pig, but closer to the latter than the former. The canine flanges are more prominent than in the wild boar, and in profile the symphysis is flat or concave rather than slightly convex, as is the case with *Sus scrofa*. The back of the symphysis is about level with P₃, whereas in *Sus scrofa* it is level with P₂, but the small shelf developed in the bush pig for the insertions of the genioglossus and geniohyoideus muscles is not apparent. The mandibular ramus is thicker than in *Sus scrofa* and has a swollen appearance lateral to M₁ and M₂, as in the forest hog and in *Kolpochoerus limnetes*. The incisors are broken but were generally like those of *Sus scrofa* or *Potamochoerus porcus*. The P₃ and P₄ are narrow cutting teeth, with P₃ very *Sus*-like. In P₄ (which is lying obliquely in the tooth row) the displacement of the central cusp is not as marked as in *Sus scrofa*, but it is also not as stout a tooth as in the bush pig. The first and second molars have less complex folding than in *Sus scrofa* and are more like those of the bush pig. However, the third molars are further simplified and the lateral columns are more distinct than in the bush pig and the outer walls of the main pillars are smoothly rounded, although the basic structure is still close to *Potamochoerus porcus* in respect of the number of columns present and in the limited development of the talonid.

Other material from the members DD and KH serves to confirm that AL 134-7 is a reasonably representative specimen. However, in a few of the third molars the large terminal pillar is accompanied by a second, smaller one. AL 157-2 (DD-3/KH-1) also includes the symphysis with broken incisors and canines, and this specimen also lacks any evidence for a lower P₁ in the diastema; the cheek teeth are too damaged to be informative. AL 116-60 (DD-2/3) is a right mandibular ramus with RM₁₋₃ well preserved and a fragment of the left ramus with LM₃. In this specimen the teeth are distinctly simpler in enamel folding, and the columnar laterals have a smooth, rounded external face, with thick enamel.

The Larger Specimens

Five specimens differ sufficiently in size from the other material to warrant special consideration. Three are from DD-1 and are: AL 287-1A, a left mandibular ramus with LP₃-M₂ and part of LM₃; AL 296-1, a damaged mandible with the symphysis and some intact teeth; AL 325-8, a left mandibular ramus with LP₄-M₂. From DD-1/2 there is a fragment of mandible with LM₃, AL 182-48, and from KH-1/2 a fragment of maxilla with RM³, AL 310-12. In Figs. 8 and 9 the plots for these specimens have been circled. The RM³ lies just over two standard deviations from the mean for the remainder of the sample. The mean for the four lower third molars is almost exactly two standard deviations

distant from the mean for the remaining sample, but lies closely along the same regression line. Similar size differences apply to the other teeth, which is simply consistent with the fact that they belonged to larger-than-average individuals.

From a morphological point of view, the third molars in these specimens have thick enamel and the secondary fissures are merely thin cracks, while the main lateral pillars tend to be columnar and have smooth, rounded external faces. In all these respects, the teeth resemble those of *Kolpochoerus limnetes*, especially the material from the lowest members in the Omo sequence. However, the crown still consists of only two pairs of laterals and a single large median terminal pillar, whereas in *K. limnetes* there is normally a third lateral pillar on the lingual side in the uppers and on both sides in the lowers; in some early specimens, the third pair of laterals constitutes the terminal talonid, in place of the single median terminal pillar. Clearly these larger specimens point towards *K. limnetes*, while retaining the basic characteristics defined for the species *afarensis*. This is what one might expect if the latter is ancestral to *limnetes*, as seems very probable, and it is perhaps natural that the larger specimens should be most *limnetes*-like.

Discussion

The discovery of this small suid is of particular interest in furnishing a possible clue to the ancestry of the living bush pig, which is almost unknown as a fossil until the later Pleistocene. It may also provide a very reasonable ancestor for *Kolpochoerus limnetes*, whose primary origin has been uncertain. On purely dental grounds, the small Hadar suid might have been placed almost equally well in either *Sus* or *Potamochoerus*, although perhaps with a bias towards the latter, but the structure of the zygomatic arches is very different from that of *Sus* and so like that of *Kolpochoerus* that it is logical to assign it to the latter genus. There is a basic, but not exact, resemblance to the zygoma in the bush pig.

Consideration must be given to the possibility that *Kolpochoerus afarensis* is actually the direct ancestor of the living *P. porcus*, or even that it should be regarded merely as a fossil representative of that species. It has not been regarded here as a synonym of *P. porcus* because of the following considerations:

(a) the mutual relationships between the premolars and molars are different and have the same proportions as in *Sus scrofa*: P¹ is present in the adult, which is rare in bush pig, and P¹ and P² are virtually the same as in the wild boar, P¹ being almost as big as P² in the bush pig; M³ is larger than in the bush

pig but the same size as in *Sus scrofa*. Similar relationships apply to the lower dentition.

(b) the premolar morphology is somewhat different from that of *Potamochoerus porcus*, not only in the rather more sectorial character of the second and third premolars, but also in the possession of a *Sus*-like displaced double crest in P₄. The P₄ is more *Sus*-like and, despite the variability of this tooth encountered in living suids, the difference must be regarded as grounds for not placing the fossil into *Potamochoerus*.

(c) the molar teeth in the fossil tend to have thicker enamel and less folding than in the living bush pig. This would suggest some degree of specialization away from a bush-pig-like tooth rather than a truly ancestral type. However, the earliest specimens have molar teeth that are most like those of *P. porcus*, and thus early *Kolpochoerus afarensis* may well be very close to the branching point. Modification of the premolars would doubtless take place during the descent of *P. porcus*, leading to its present characteristics. It seems likely that the premolar characteristics that help to separate *Potamochoerus porcus* from *Sus* are not fully developed and it might be inferred that a still earlier ancestor might well be even more *Sus*-like in the premolar dentition. There is thus no particular reason to demand descent of *Potamochoerus* from *Pro-potamochoerus*.

As far as *Kolpochoerus limnetes* is concerned, *K. afarensis* seems to be a very suitable ancestor, with the degree of resemblance increasing in the higher stratigraphic horizons. It could be argued that it should therefore be placed in that species as a very early representative and that a distinction based on the number of lateral columns in the third molars is too arbitrary to be valid. Of course, in a more-or-less unbroken lineage of this type it is indeed difficult to draw a hard and fast boundary and any definition must be somewhat arbitrary. The literature teems with arguments about the problems involved in attempting to subdivide a continuously evolving lineage, especially in the absence of those frequent time gaps that often serve so conveniently to break up stratigraphic sequences into neat and manageable parcels. As W. S. McKerrow (1956) has pointed out, it is necessary "to realise that specific names in palaeontology are frequently only applicable to fixed points in a plexus of evolving organisms." Extension of a single species name to a morphologically changing complex over a long period of time avoids (or evades) the problem, but ceases to be useful when the end members in the lineage are so different that it is almost inconceivable that they would, or could, belong to the same biospecies if they had lived at the same time. As T. Neville George (1956) put it: "If a spade were always called a spade no doubt correlation would be greatly eased, though it might not be very exact if the spade were anything from a steam shovel to a

teaspoon." Palaeontological nomenclature should be stratigraphically useful as well as biologically reasonable. Accordingly, the present writer prefers to define *Kolpochoerus afarensis* as a species, recognizing that it will grade into *K. limnetes* and that some specimens may have to be dealt with by indicating their borderline character (easily done by use of the prefix *aff* with one of the species names). *K. afarensis* is thus regarded as close to the point of divergence of the *P. porcus* and *P. limnetes* lineages. Perhaps also belonging to this species are two third molars from Laetolil, Tanzania, described and figured by Dietrich (1942, figs. 150, 157) as *Potamochoerus* sp. cf. *major*.

DISCUSSION

The identifiable material assigned to each of the three species described here has been analysed in Table 4 to show the numbers of specimens from each stratigraphic submember, divided into upper and lower dentitions. Much fragmentary material has been omitted. On the right are shown the total numbers of specimens for each stratigraphic subdivision. It should be borne in mind that the units do not represent equal intervals of time and, accordingly, that the numbers do not represent original relative abundances. It is of interest to note that for each of the species, skulls and upper dentitions make up only one quarter to one third of the material, while the lower jaws and teeth are much better represented.

From a stratigraphic viewpoint, *Nyanzachoerus pattersoni* is almost confined to the Lower Sidi Hakoma member, with only three specimens from the Upper Sidi Hakoma. One isolated upper third molar from locality AL 134 is supposedly from DD-2/3 and if this is correct, then *N. pattersoni* still existed at that level, but it might be a derived or misplaced specimen. In the lower Sidi Hakoma member, *Notochoerus euilus* is almost as abundant as *Nyanzachoerus*, but *Kolpochoerus afarensis* is slightly less abundant, making up one quarter of the suid sample from this level. In the Denen Dora member, where *Nyanzachoerus* is effectively absent, *Notochoerus euilus* makes up 75% of the suid material and *Kolpochoerus afarensis* maintains its proportion of 25% of the suid sample. From the Kada Hadar there are too few suids for numbers to be significant, but both *Notochoerus euilus* and *Kolpochoerus afarensis* are represented.

As far as comparison with other sites is concerned, the *Nyanzachoerus pattersoni* material matches very closely with the sample from Kanapoi, where the age is estimated as close to 4.0 million years. The *Notochoerus euilus* material is generally similar to the large sample from the Usno Formation in the Omo area, which has an estimated age of close to 3.0 million years. However,

TABLE 4
Stratigraphic distribution of Hadar suid specimens
(individuals – upper and lower elements)

Stratigraphic Unit	<i>Nyanzachoerus pattersoni</i>		<i>Notochoerus euilus</i>		<i>Kolpochoerus afarensis</i>		Upper	Lower	Total
	Upper	Lower	Upper	Lower	Upper	Lower			
KH-2/3	—	—	—	—	—	2	0	2	2
KH-2	—	—	1	—	—	—	1	0	1
KH-1/2	—	—	—	2	1	1	1	3	4
KH-1	—	—	—	1	—	1	0	2	2
DD-3/KH-1	—	—	1	2	—	1	1	3	4
DD-3	—	—	5	11	3	9	8	20	28
DD-2/3	1?	—	11	24	2	4	14	28	42
DD-2	—	1	11	25	7	6	18	32	50
DD-1/2	—	—	5	23	—	—	5	23	28
DD-1	—	—	1	9	2	4	3	13	16
SH-4/DD-1	—	—	3	2	—	—	3	2	5
SH-4	2	1	3	7	1	2	6	10	16
SH-3/4	—	1	—	2	—	—	0	3	3
SH-3	1	1	2	2	—	2	3	5	8
SH-2/3	—	—	1	6	—	1	1	17	8
SH-2	6	9	—	4	2	7	8	20	28
SH-1/3	—	14	1	7	3	4	4	25	29
SH-1	—	4	1	5	1	3	2	12	14
Basal	—	1	—	—	—	1	0	2	2
HS	—	1	—	—	1	1	1	1	2
Uncertain	—	—	1	4	—	—	2	4	6
Totals	10	32	47	136	24	49	81	217	298
As % of species	23.8	76.2	25.7	74.3	32.9	67.1	27.2	72.8	
Summary									
Kada Hadar	0	0	2	5	1	3	3	10	13
Denen Dora	1?	1	33	92	14	23	48	116	164
Upper Sidi									
Hakoma	3	3	8	13	1	4	12	20	32
Lower Sidi									
Hakoma	6	27	3	22	6	15	15	64	79
Miscellaneous	0	1	1	4	2	2	3	7	10
As % of Grand Total	3.4	10.7	15.8	45.6	8.1	16.4	27.2	72.8	
	14.1%		61.4%		24.5%		100.0%		

the Hadar material from the Sidi Hakoma member seems to be a little more "primitive" and closer to its presumed ancestor, *Nyanzachoerus jaegeri*. An age for the Sidi Hakoma member of 3.0–3.5 million years would give a better fit than the 2.9–3.0 m. y. age presently obtained from the basalt, while an age close to 3.0 million years for the Denen Dora member would be best in line with the stage of evolution of the *Notochoerus euilus* material. Thus, the suid evidence confirms in general the age provisionally assigned to the Hadar Formation but suggests that the lower part may be a little older than the present radiometric determinations indicate.

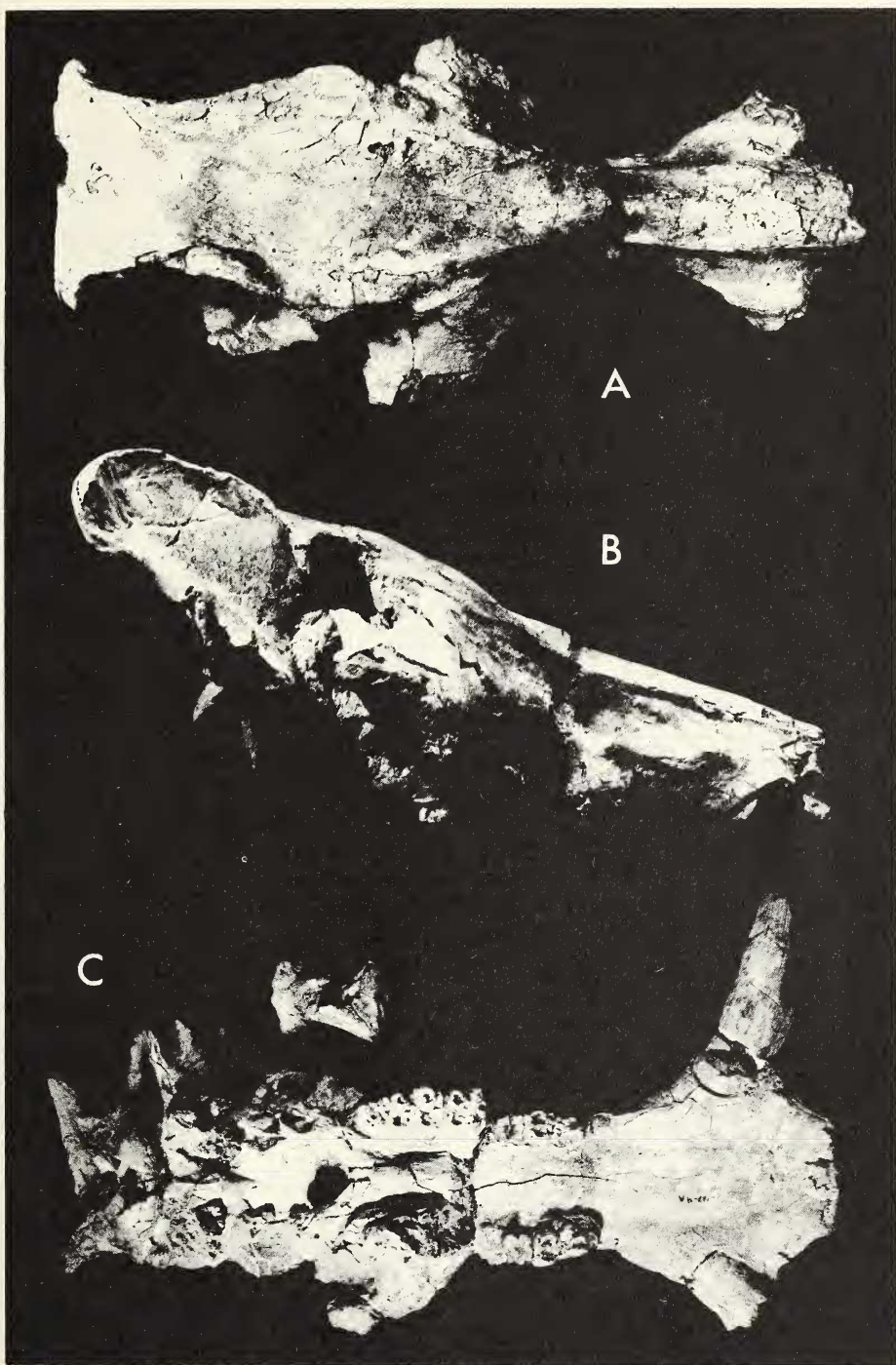


Plate 1. *Nyanzachoerus pattersoni*, male AL 137-4, dorsal (A), right lateral (B) and palatal views. One-fifth natural size.

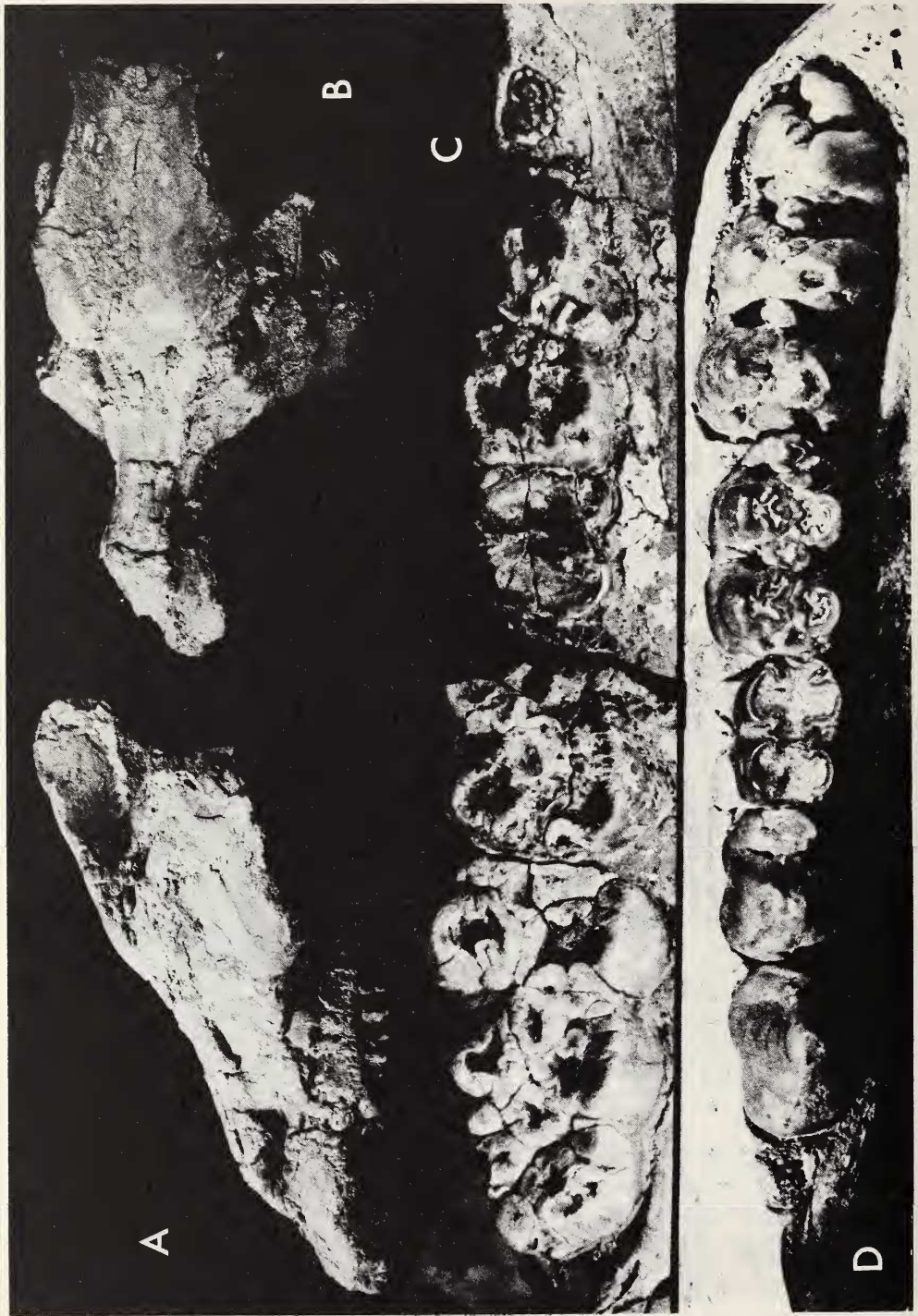


Plate 2. *Nyanzachoerus pattersoni*. A, left lateral, and B, dorsal, views of female, AL 107-13, one-fifth natural size. C, right upper cheek teeth of male AL 137-4 (with dislocation seen in plate 1 B removed photographically), natural size. D, left lower cheek teeth, AL 126-8, natural size.

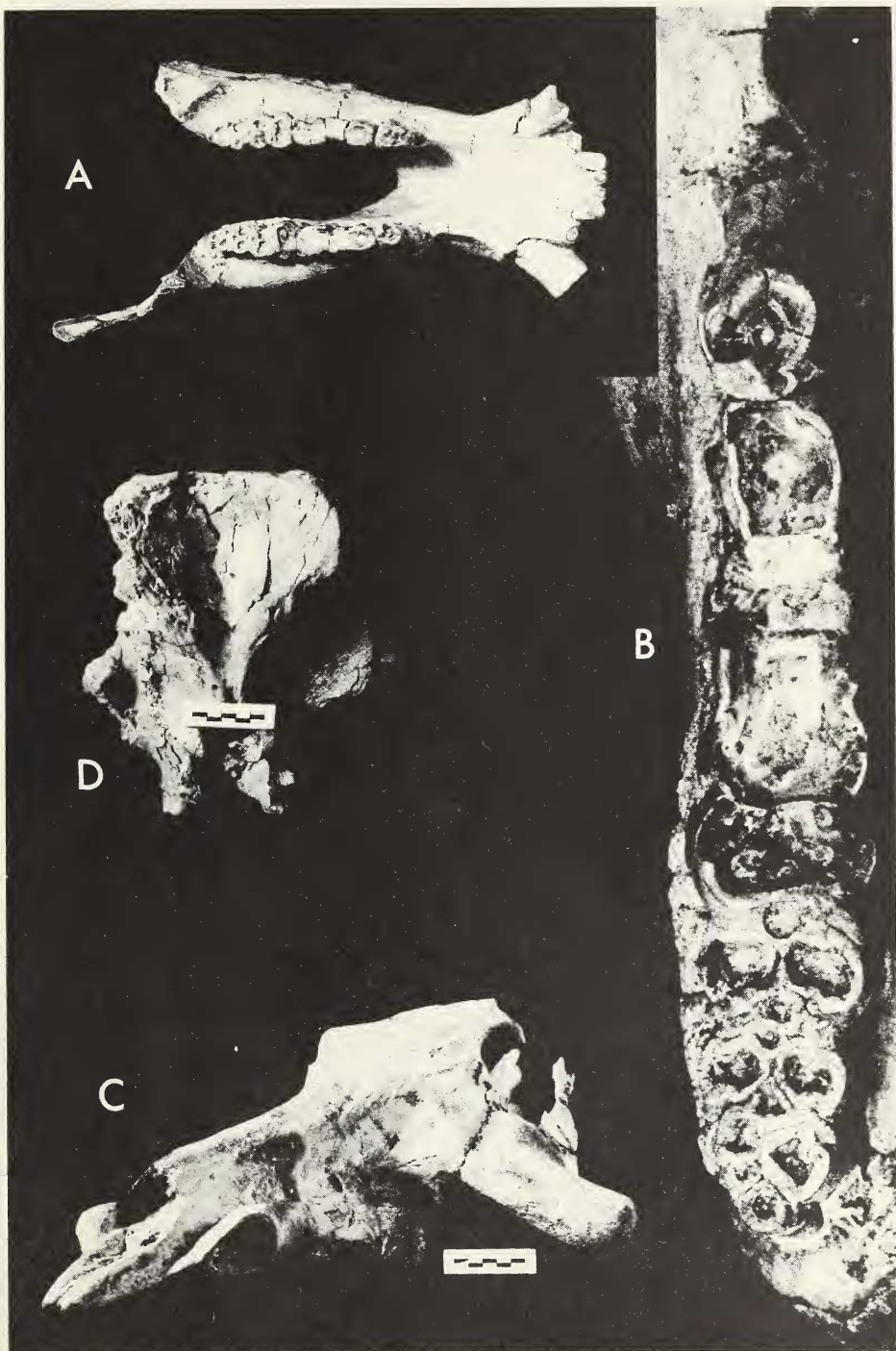


Plate 3. *Nyanzachoerus pattersoni*, AL 218-2: A, mandible of old individual, one-fifth natural size; and B, right lower cheek teeth, natural size. *Notochoerus euilus*, AL 172-1: C, oblique view to show the form of the zygomatic protuberances; D, occiput, one-fifth natural size.

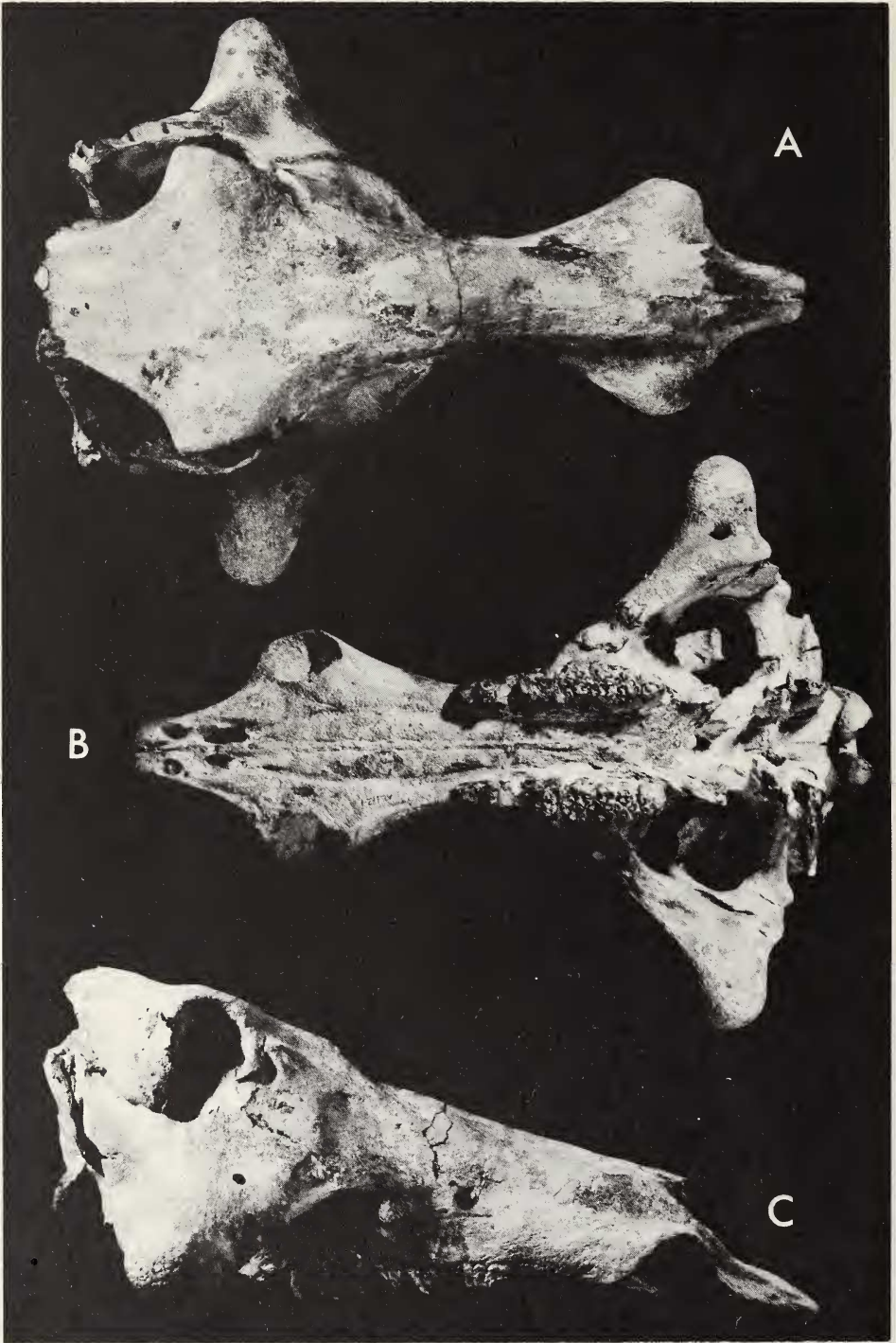


Plate 4. *Notochoeris eutilus*, AL 172-1, dorsal (A), palatal (B), and right lateral (C) views, one-fifth natural size.



Plate 5. *Notochoerus euilus*, AL 172-1, palate and cheek teeth on both sides. Natural size.



Plate 6. *Notochoeris euilius*, upper right cheek teeth. A, very young adult, AL 108-3; B, AL 167-15, adult with RP⁴ damaged; and C, intact LP⁴ showing the posterior cingulum development; D, AL 116-93. All natural size.

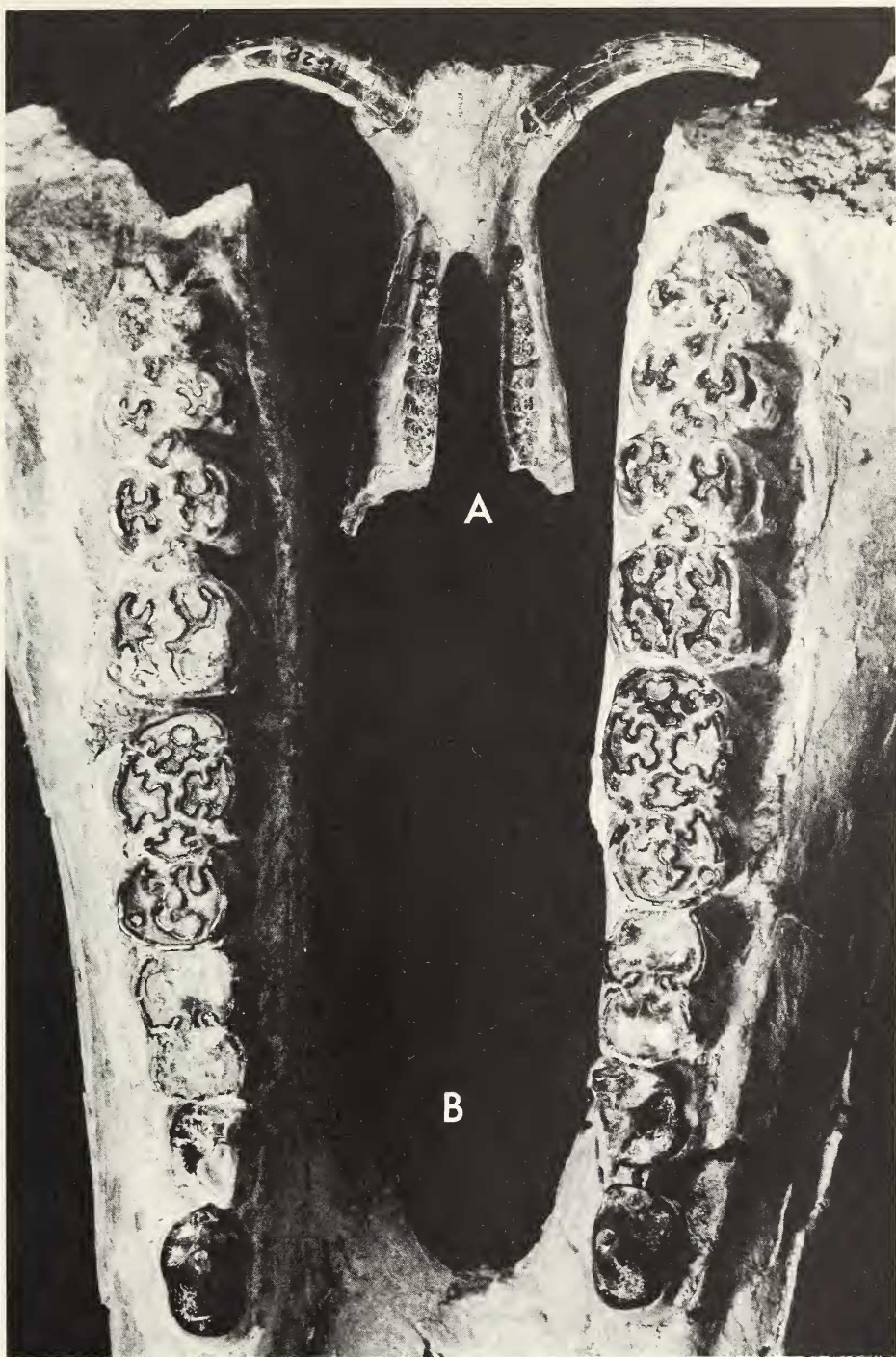


Plate 7. *Notochoerus euilus*, AL 116-28. A, mandible with both incisors, one-fifth natural size; B, cheek teeth of both sides, natural size.

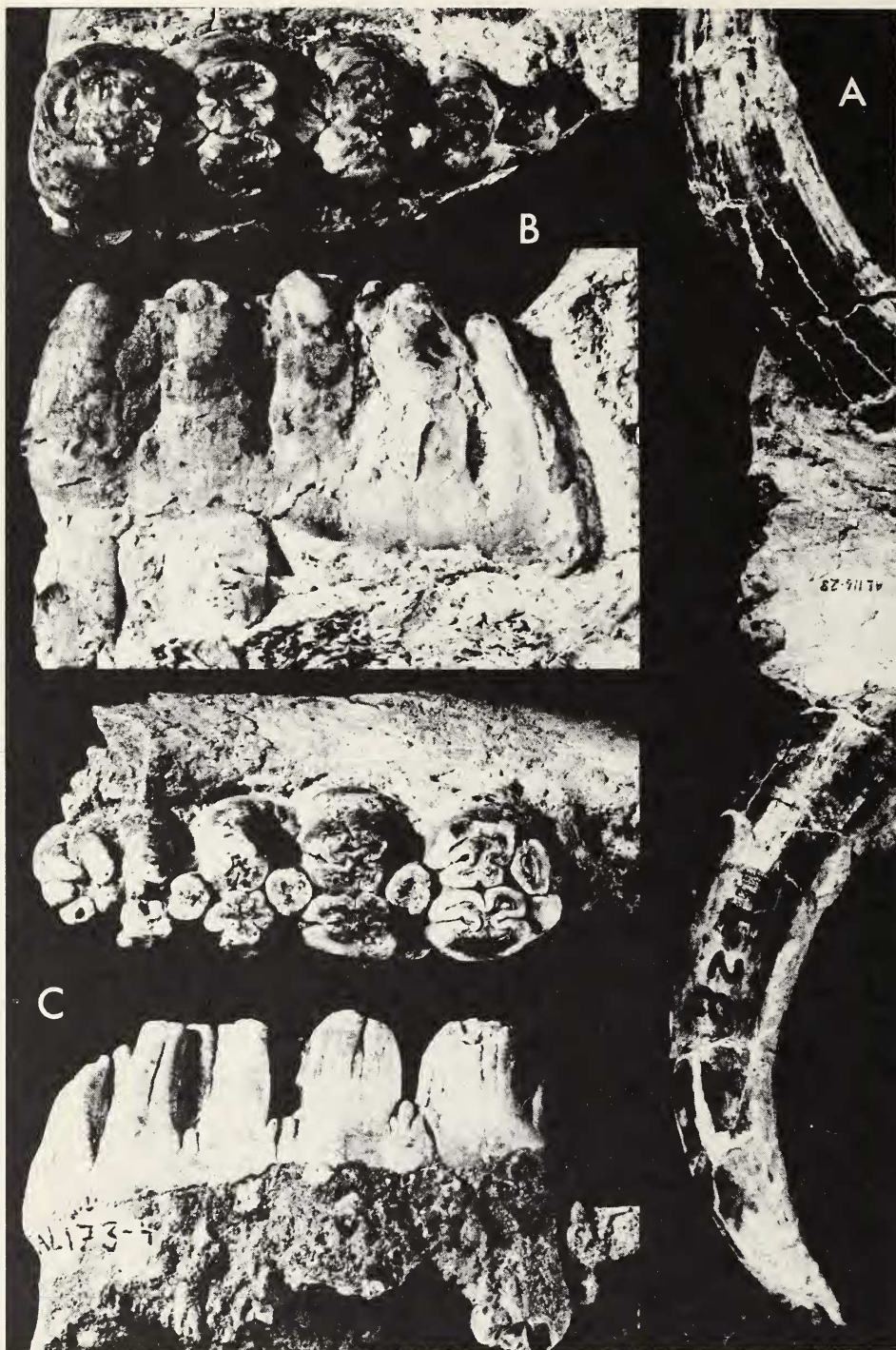


Plate 8. *Notochoerus euilus*. A, anterior border of symphysis with $L1_{2,3}$ intact and roots of other incisors, one-half natural size. B, AL 122-5, LM_3 in early wear, occlusal and outer lateral views, natural size; C, AL 173-4, LM_3 in moderate wear, inner lateral and occlusal views, natural size.



Plate 9. *Kolpochoerus afarensis*, Holotype, AL 147-10, left lateral (A) and palatal (B) views, one-third natural size.



Plate 10. *Kolpochoerus afarensis*. A, palate and cheek teeth of Holotype, AL 147-10. B, palate with P³-M² on both sides, AL 116-1. Natural size.

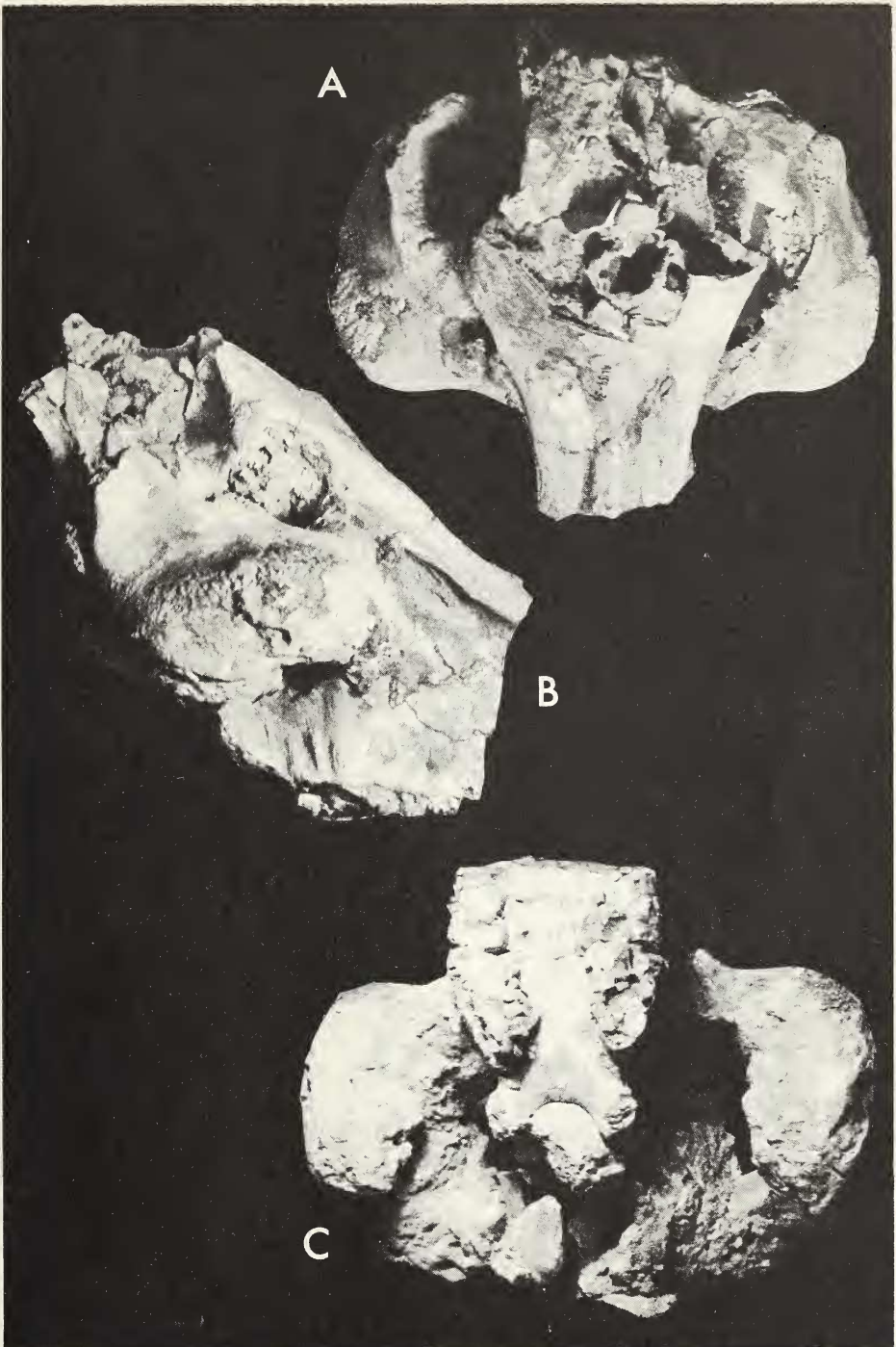


Plate 11. *Kolpochoerus afarensis*. AL 154-34, partial cranium of old individual, dorsal (A), right lateral (B), and palatal (C) views. One-third natural size.



Plate 12. *Kolpochoerus afarensis*. A, palate of juvenile, AL 224-3, with canines erupting, RP¹ and M¹⁻² on both sides; B, AL 109-1, left mandibular ramus with broken canine, socket of LP₁ near canine, roots of LP₂₋₃ and LM₁, LP₄, LM₂₋₃ intact. All natural size.

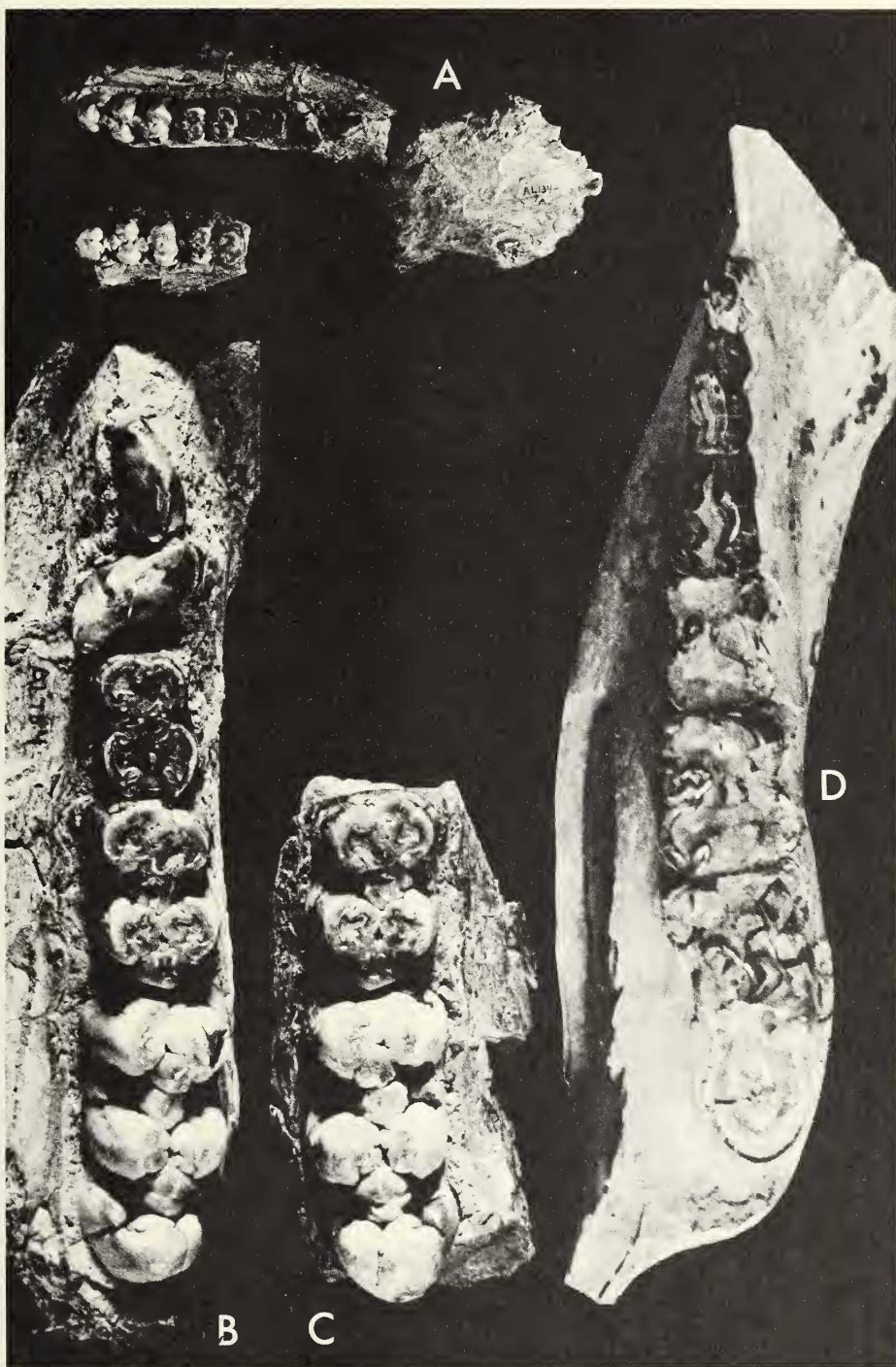


Plate 13. *Kolpochoerus afarensis*. A, AL 134-7, incomplete mandible with good symphysis, one-fifth natural size; B, left cheek teeth of A, showing the oblique LP₄, and C, right M₂₋₃, natural size; D, AL 186-20, left mandibular ramus with good LP₂₋₄ and well-worn LM₁₋₃, natural size.

REFERENCES

- Aronson, J. L., T. J. Schmitt, R. C. Walter, M. Taieb, J. J. Tiercelin, D. C. Johanson, C. W. Naeser, and A. E. M. Nairn, 1977, New geochronologic and paleomagnetic data for the hominid-bearing Hadar formation of Ethiopia, *Nature*, London, 267: 323–327.
- Broom, R., 1925, On evidence of a giant pig from the late Tertiaries of South Africa, *Records Albany Mus.*, 3: 307–308.
- Cooke, H. B. S., 1976, Suidae from Plio-Pleistocene strata of the Rudolf basin, in *Earliest man and environments in the Lake Rudolph Basin*, edited by Y. Coppens, F. C. Howell, G. L. Isaac, and R. E. F. Leakey, Chicago: University of Chicago Press, 251–263.
- Cooke, H. B. S. and S. C. Coryndon, 1970, Pleistocene mammals from the Kaiso Formation and other related deposits in Uganda, *Fossil Vertebrates of Africa*, 2: 109–224.
- Cooke, H. B. S. and R. F. Ewer, 1972, Fossil Suidae from Kanapoi and Lothagam, northwestern Kenya. *Bull. Mus. Comp. Zool.*, Harvard, 143 (3): 149–295.
- Coppens, Y. 1971, Une nouvelle espèce de suidé du Villafranchien de Tunisie, *Nyanzachoerus jaegeri* nov. sp., *C. R. Acad. Sci. Paris*, 272D: 3264–3267.
- Dietrich, W. O., 1942, Ältesquartäre Säugetiere aus der südlichen Serengeti, *Deutsch-Ost-Afrika, Paläontographica*, 94A: 43–133.
- Ewer, R. F., 1958, The fossil Suidae of Makapansgat. *Proc. Zool. Soc. London*, 130: 329–372.
- George, T. N., 1956, Biospecies, chronospecies and morphospecies, in *The species concept in palaeontology*, by P. C. Sylvester-Bradley (ed.), London: The Systematics Society, 1956: 123–137.
- Hoepen, E. C. N. and H. E. van, 1932, Vrystaatse wilde varke, *Paleont. Navors. nas. Mus. Bloemfontein*, 2 (4): 39–62.
- Hopwood, A. T., 1926, Fossil mammalia, in *The geology and palaeontology of the Kaiso Bone Beds*, by E. J. Wayland, *Occ. Pap. Geol. Surv. Uganda*, 2: 13–36.
- Hünemann, K. A., 1968, Die Suidae (Mammalia, Artiodactyla) aus den Dinotheriensanden (Unterpliozän = Pont.) Rhein Hessens (Südwestdeutschland), *Schweiz. palaeont. Abh.* 86: 1–96.
- Johanson, D. C. and M. Taieb, 1976, Plio-Pleistocene hominid discoveries in Hadar, Ethiopia, *Nature*, London, 260: 293–297.
- Johanson, D. C., M. Taieb, B. T. Gray, and Y. Coppens, 1978, Geological framework of the Pliocene Hadar Formation (Afar, Ethiopia), with notes on paleontology including hominids, in *Geological background to fossil man*, by W. W. Bishop (ed.), Edinburgh: Scottish Academic Press.

- Leakey, L. S. B., 1958, Some East African Pleistocene Suidae, Fossil Mammals of Africa, No. 14, British Mus. (Nat. Hist.): 1-133.
- McKerrow, W. S., 1956, Fossil species and the rules of nomenclature (Discussion), in The species concept in palaeontology, by P. C. Sylvester-Bradley (ed), London: The Systematics Society, 1956, p. 122.
- Taieb, M., 1974, Évolution Quaternaire du bassin de l'Awash (Rift éthiopien et Afar), Université de Paris VI, doctoral thesis, Vol. 1—Text, 390 pp., Vol. 2—Plates and maps.
- Taieb, M., Y. Coppens, and D. C. Johanson, 1972, Dépôts sédimentaire et faunes du plio-Pléistocène de la basse vallée de l'Awash (Afar central, Éthiopie), C. R. Acad. Sci. Paris, 275D: 819-822.
- Taieb, M., D.-C. Johanson, Y. Coppens, and J. L. Aronson, 1976, Geological and palaeontological background of Hadar hominid site, Afar, Ethiopia, Nature, London, 260: 293-297.